FURTHER STUDIES ON THE INHERITANCE OF "ROGUE" TYPE IN GARDEN PEAS (PISUM SATIVUM L.)

By

WILBER BROTHERTON, JR.

A Thesis Presented in Partial Fulfillment of the Requirements for the Degree of Doctor of Philosophy at the University of Michigan.

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FURTHER STUDIES ON THE INHERITANCE OF "ROGUE" TYPE IN GARDEN PEAS (PISUM SATIVUM L.)[1]

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INTRODUCTION

Since the rediscovery of Mendel's classical paper on heredity, characters of the garden pea (*Pisum sativum*) have been used to illustrate typical Mendelian inheritance. In 1915 Bateson and Pellew (*1*) [2] published an account of the genetics of types of peas known as "rogues"—types in which heredity has thus far appeared to be non-Mendelian. This paper was followed by later publications (*2*, *3*) dealing especially with variations in the proportion of rogues obtained from seeds from different parts of the same intergrading intermediate plant. Briefly stated, the facts reported were as follows:

(*a*) Certain varieties of the garden pea, such as Early Giant, Ne Plus Ultra, and Duke of Albany, are characterized by broad, wavy stipules and leaflets, both having rounded, emarginate apices and broad, straight pods. Occasionally there occur in pure-lines of such varieties plants called "rogues" that are described as "wild" or "vetch-like." The rogues differ from the parent form mainly in the reduction in width of the foliar parts (stipules and leaflets) and of the pods. The stipules of the rogues are narrow and pointed; the pods are narrow and curved along the upper suture. Rogues are not produced with any definite regularity or in such numbers that a characteristic ratio can be established between the rogues and parent form.

(*b*) Between the parent types and the vetch-like rogue are found intermediate forms, especially in the variety Early Giant. The intermediates are of several classes and may grade almost insensibly into types or rogues. The most usual form is characterized by broad foliage in the early stages of development, but as the plant matures the stipules become pointed and more roguelike. Such a plant is called by Bateson and Pellew an intergrading intermediate. Genetically there are two kinds of intermediates: (1) Those whose progeny consists of many rogues and few intermediates; and (2) those whose progeny consists of few rogues and many intermediates. The rogues from both kinds of families breed true, while the intermediates tend to produce rogues and intermediates in proportions comparable to those of their parents, i. e., there are high and low rogue-producing strains. Nevertheless, no regular ratio of rogues to intermediates can be found in successive generations.

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[1] Accepted for publication Jan. 18, 1923. This contribution records cooperative work between the Bureau of Plant Industry and the University of Michigan which was carried on at the Department of Botany, University of Michigan.

[2] Reference is made by number (italic) to "Literature cited," p. 852.

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(*c*) Any zygote derived from the fusion of a type gamete with a rogue gamete, whichever way the cross is made, produces a rogue; an intermediate gamete on union with a type gamete produces an intermediate or nonrogue form.

(*d*) Rogues are apparently produced more often from the upper (roguelike) portion of the intermediate plants than from the lower (typelike) part. It is also found that pollen grains produce a greater ratio of rogue gametes to nonrogue gametes than do the ovules, and that the proportion of rogue gametes produced by the pollen grains increases more rapidly, in going from the lower to upper flowers, than the proportion of rogue gametes produced by ovules.

(*e*) Intergrading intermediates of strains not throwing many rogues were found to produce rogues no more often from pods of the upper parts of the plant than from the lower nodes.

(*f*) Rogues with narrow, pointed stipules and narrow, curved pods, from whatever source, breed true.

(*g*) The cross rogue × type, no matter how made, produces only rogues in the F_1 and succeeding generations. In the seedling stage of the F_1 hybrid until the seventh or eighth node is developed, many of the plants are typelike in the character of the stipules and leaflets. These plants at maturity, with few exceptions, are all rogues. The plants in the F_2 generation are recognizable as rogues at all stages of development. There is apparently no segregation in the F_1 hybrids, at sporogenesis, of the rogue and type factors.

(*h*) Intervarietal crosses of rogue with type plants of varieties producing rogues give results similar to crosses of rogue with the variety from which the rogue originated as far as the rogue characters are concerned. Side by side with the apparently non-Mendelian behavior of the rogue characters is found the expected Mendelian segregation of such characters as pod shape, color of seed, shape of seed, and height of plant.

Bateson and Pellew (1) have suggested in explanation of the anomalous genetic behavior of the rogue characters that they are due to somatic segregation of the type "elements" in the F_1 hybrid so that the type "elements" are missing from the germ plasm at the time of gamete formation. Intergrading intermediates are assumed to be mosaics of type and rogue tissue, rogue gametes being formed from rogue tissue and type gametes from type tissue.

The present paper is in part a confirmation of the above results. However, a different interpretation of the results is advanced. In addition, data are submitted of the F_1, F_2, and F_3 generations of intervarietal crosses of rogue and type plants with type plants of varieties that apparently do not produce rogues. These crosses have given entirely new results, from which important conclusions have been drawn.

EXPERIMENTAL METHOD

The experimental methods used in the work here reported were the same as those described in a previous paper (*4*). At that time the fact of cross-pollination of rogue flowers by bumblebees was noted. In growing large cultures of peas it is impossible to protect all the individual flowers with paper or cloth coverings. In 1921 an attempt was made to grow peas under wire mosquito netting. This method is too expensive to be used on a large scale, so that in the future it seems advisable to carry on as much as possible of the breeding work with rogues in the greenhouse during the winter.

The results of 1919 and 1920 may be used to illustrate the amount of volunteer crossing that may be expected in the field in crosses between Gradus and Rogue. The number of volunteer hybrids is sufficiently great to make necessary some sort of protection of the rogue plants.

In 1919, 2,932 F_2 plants of the crosses Gradus rogue with Gradus (Table II) were grown. Of the 2,932 plants, 65, or 2.3 per cent, were volunteer crosses made by insects in 1918. The out-crosses were detected by the appearance of such dominant Mendelian characters as smooth seed, blunt pods, and colored flowers in F_2 cultures that should have contained only recessives for the three characters mentioned. Any crosses inter se, or out-crosses with recessive strains, could not be detected, but, apart from a few plants of Early Giant and of Peter Pan, no varieties which did not exhibit one of the three dominant characters were planted in the experimental garden in 1918. In 1920, 3,475 F_2 and F_3 plants of the cross rogue with type (Tables II, III and IV) were raised. Among them were 42 plants of obviously foreign origin, or about 1.2 per cent, showing that the amount of volunteer crossing was considerably less in 1919 than in 1918.

Occasional volunteer crosses have been found among the rogues and intermediate rogues, but no count has been kept. However, only one case of cross-pollination by insects has been noted among the thousands of typical Gradus plants grown.

Plants used in crosses have been previously inbred for at least one generation. The rogues used were either picked from commercial plantings of Gradus or arose de novo in pure cultures of Gradus plants. In either case the rogue strains were identical and gave the same results in crosses.

Uncontrolled cross-pollination in Pisum on the scale reported here was unlooked for at the beginning of these experiments and no steps were taken to insure self-pollination. By the time it was realized that rogues were an exception to the general rule that self-pollination is invariable in Pisum it was too late to protect the hybrid rogue plants in 1919. Aside from the writer's own experience with self-pollinating varieties of peas, his garden technic was of course influenced by the general conclusion of geneticists and practical horticulturists that peas are normally self-pollinated. White (*15*) found no cross with peas having yellow cotyledons among 10,000 seeds with green cotyledons grown at the Brooklyn botanic garden.

BEHAVIOR OF GRADUS ROGUES WHEN CROSSED WITHIN THE GRADUS STRAIN

F_1 GENERATION OF CROSSES BETWEEN GRADUS AND GRADUS ROGUE

In a former publication (*4*) the results in the F_1 generation of crossing typical Gradus with Gradus rogue [3] are reported.

The F_1 seedlings were variable in regard to stipule shape, showing gradations from typelike to roguelike plants. At maturity with one exception the F_1 plants were all rogues.

In addition to the hybrids between rogue and type previously listed by the author (*4*), 134 F_1 plants from 37 other crosses were grown, making a total from all sources of 282 F_1 plants of the cross Gradus × Gradus rogue, and reciprocal. Of the 282 plants all but three were classified as rogues at maturity.

[3] The name "Gradus rogue" or "Rogue" as used throughout this paper refers to the same type of mutation as that previously referred to (*4*) as a "Rabbit-ear" Rogue.

Two of the exceptional plants occurred in a single F_1 culture,[4] of which two plants were thorough rogues, while two others were intergrading intermediates, i. e., they were typelike at the lower nodes, but at upper nodes the stipules were pointed but much broader than in typical rogues. In the F_2 generation the progeny of the intergrading intermediates consisted of 32 and 33 rogues, respectively.

The third exceptional plant among the F_1 of rogue × type was described in 1919 (*4*). Its offspring in 1919 consisted of 19 intergrading intermediates and 15 type plants. The same cross and its reciprocal produced 7 other F_1 plants, described as rogues at maturity. From the character of the F_2 progenies (Table I) it is probable that the F_1 plants were in reality extreme intergrading intermediates, as the F_2 is characteristic of the progeny of intergrading intermediates. The plants behaved as intergrading intermediates of the sort described by Bateson and Pellew (*1*) as producing types, intergrading intermediates, and few or no rogues.

TABLE I.—*F_1 and F_2 generation of atypical hybrids of Gradus rogue × Gradus type and reciprocal*

1919 culture No.	Pedigree.	F_2		
		Rogues.	Intergrading intermediates.	Types.
9.1207	(G13-1-6-1t×G19-1-3r)—1	0	27	0
9.1208	(G13-1-6-1t×G19-1-3r)—2	0	23	0
9.1209	(G13-1-6-1t×G19-1-3r)—3	0	9	2
9.1210	(G13-1-6-1t×G19-1-3r)—4	0	0	23
9.1216	(G19-1-3r×G13-1-6-1t)—1	2	8	3
9.1217	(G19-1-3r×G13-1-6-1t)—2	0	27	0
9.1218	(G19-1-3r×G13-1-6-1t)—3	0	0	4
9.1219	(G19-1-3r×G13-1-6-1t)—4..Type foliage	0	19	15

F_2 AND F_3 GENERATIONS OF CROSSES BETWEEN GRADUS AND GRADUS ROGUE

From 184 F_1 hybrids of Gradus × Gradus rogue and reciprocal 4,319 F_2 plants were raised in 1919 and 1920. In the seedling stage the greater portion were easily recognizable as rogues; others could be termed intermediates, but none showed the typelike appearance found among the F_1 seedlings. (Among the 4,319 plants shown in Table II, 81, or 1.8 per cent, were from foreign pollination, as explained elsewhere in this paper. The volunteer out-crosses were generally distinguished in the seedling stage as plants with typelike stipules.) At maturity the plants were either rogues or various sorts of intermediates. Thirty-nine F_2 rogues gave in the F_3 generation 575 plants, all rogues except five plants (0.8 per cent). The products of volunteer out-crossing in 1919 are shown in Table III.

[4] The intergrading intermediates were plants No. 3 and No. 4 of cross (G10-1-12-1t×G23-1-1-16r) in the F_1 generation.

TABLE II [a].—*Gradus rogue × Gradus type and reciprocal in the F_2 generation*

Culture No.	Rogues.	Crosses.
1919:		
9.1200	10	
9.1201	3	
9.1202	13	
9.1203	16	
9.1204	4	
9.1205	10	
9.1206	3	
9.1211	29	
9.1212	39	
9.1213	36	
9.1214	35	
9.1215	54	2
9.1220	4	
9.1221	4	
9.1222	2	
9.1223	2	
9.1226	12	
9.1227	14	
9.1251	80	
9.1252	82	
9.1253	86	
9.1254	10	
9.1255	208	
9.1265	37	3
9.1266	27	
9.1267	24	
9.1268	51	1
9.1269	15	1
9.1270	37	
9.1271	39	
9.1272	47	
9.1273	28	
9.1274	27	3
9.1275	34	4
9.1276	57	3
9.1277	54	
9.1278	43	1
9.1279	6	
9.1280	19	
9.1284	118	4
9.1285	73	1
9.1286	36	
9.1287	49	1
9.1288	85	2
9.1289	22	1
9.1293	6	1
9.1294	52	4
9.1295	73	12
9.1296	54	
9.1297	19	
9.1298	17	2
9.1299	43	1
9.1300	32	
9.1301	95	
9.1302	77	7
9.1304	45	1
9.1303	15	
9.1305	71	1
9.1306	46	
1919—Continued.		
9.1307	29	
9.1308	18	
9.1309	25	
9.1316	58	2
9.1317	13	3
9.1318	44	
9.1319	73	
9.1320	108	4
9.1321	31	
9.1322	43	
9.1323	4	
9.1324	21	
9.1325	25	
9.1326	46	
Total	2,867	65
1920:		
0.89	15	2
0.90	17	1
0.91	12	
0.92	37	1
0.93	12	
0.94	7	
0.95	15	1
0.96	7	
0.97	30	
0.98	48	1
0.99	10	
0.100	6	
0.101	14	
0.102	7	
0.103	15	
0.104	14	1
0.105	14	
0.106	12	
0.107	30	
0.108	26	
0.109	10	
0.110	9	
0.112	21	2
0.113	20	1
0.114	13	
0.115	8	
0.116	18	
0.117	18	
0.118	15	
0.119	20	
0.120	22	
0.121	21	
0.122	18	
0.123	31	
0.124	12	
0.125	25	
0.126	14	
0.127	25	
0.128	22	
0.129	16	
0.130	15	

[a] In Tables II, III, and IV, unless otherwise noted, the parent plants were rogues in each instance. The column headed "Crosses" shows the number of volunteer hybrids occurring in the various cultures.

TABLE II.—*Gradus rogue X Gradus type and reciprocal in the F_2 generation*—Continued.

Culture No.	Rogues.	Crosses.	Culture No.	Rogues.	Crosses.
1920—Continued.			1920—Continued.		
0.131	36		0.199	9	1
0.184	27		0.200	32	
0.185	20		0.202	6	
0.186	23		0.203	15	
0.187	38		0.204	18	
0.188	37		0.205	30	
0.189	34		0.206	37	2
0.190	8		0.207	3	
0.191	26	2	0.208	14	
0.192	10		0.209	39	
0.193	26		0.210	36	
0.194	21		0.211	7	
0.195	31		0.212	2	
0.196	29		0.213	32	
0.197	7				
0.198	21	1	Total (1919–20).	4,238	81

TABLE III.—*Gradus rogue × Gradus type and reciprocal in the F_3 generation*

Culture No.	Rogues.	Crosses.	Culture No.	Rogues.	Crosses.
1920:			1920—Continued.		
0.371	22		0.391	10	
0.372	10		0.392	15	
0.373	23		0.393	12	
0.374	12		0.394	14	
0.375	11		0.395	16	
0.376	13		0.396	24	2
0.377	16		0.397	3	
0.378	13		0.398	25	
0.379	3		0.399	17	1
0.380	6		0.400	21	
0.381	6		0.401	18	
0.382	15		0.402	11	
0.383	10		0.403	22	
0.384	20		0.404	17	
0.385	12		0.405	18	
0.386	13		0.406	23	
0.387	17		0.407	23	2
0.388	17		0.408	18	
0.389	15				
0.390	14		Total	575	5

F_1 AND F_2 GENERATIONS OF CROSSES BETWEEN GRADUS TYPE AND THE F_1 OF GRADUS TYPE WITH GRADUS ROGUE

The cross type × (type × rogue) gave an F_1 of 88 plants which showed a wide range of variation from typelike to roguelike plants in the seedling stage, but which at maturity were all rogues. Sixty-six F_1 plants of the sesquireciprocal crosses gave an F_2 progeny (Table IV) of 1,477 rogues, 6 intermediate types, and 22 volunteer hybrids (1.4 per cent).

The exceptional intermediate types occurred in the F_2 culture 0.322, which also contained 23 rogues and 1 out-crossed plant. Seven other families from the original cross which produced culture 0.322 gave only rogues in the F_2 generation.

TABLE IV.—*Back-crosses Gradus type×(Gradus type×Gradus rogue) in F_2 generation*

Culture No.	Rogues.	Others.	Crosses.	Culture No.	Rogues.	Others.	Crosses.
1920:				1920—Contd.			
0.216	3			0.325	23		
0.217	2			0.326	16		1
0.292	36		2	0.327	22		
0.293	25			0.328	17		
0.294	23			0.329	40		
0.295	23			0.330	31		
0.296	2			0.331	41		
0.297	31			0.333	18		
0.298	18			0.334	54		1
0.299	11			0.335	22		
0.300	11			0.336	36		
0.301	38			0.338	73		
0.302	12			0.341	18		1
0.303	27			0.342	21		
0.304	1			0.343	20		2
0.305	6			0.344	6		
0.306	27			0.345	28		
0.307	17			0.346	20		
0.308	20		1	0.347	15		
0.309	20			0.348	23		
0.310	16			0.349	18		
0.311	44		4	0.350	23		
0.312	33			0.351	15		
0.313	17			0.352	30		
0.314	10			0.353	26		
0.315	44			0.355	7		
0.316	45		2	0.356	13		
0.317	38		2	0.357	18		5
0.318	7			0.358	27		
0.319	16			0.368	14		
0.320	31			0.369	22		
0.321	3			0.370	15		
0.322	23	6	1	Total	1,487	6	22
0.324	35						

STATISTICAL STUDY OF THE INHERITANCE OF STIPULE SHAPE IN GRADUS ROGUE AND GRADUS TYPE

In order to get a more exact comparison of the rogues and types, on the one hand, and the F_1 and F_2 generations of hybrids between the two, measurements of the length and width of the stipules from the fourth to the ninth node were made in the various categories of plants. The ratio of width to length of stipule was then calculated. Because of disease and mechanical injury the same number of stipules could not be measured at each node in each group of plants. The class frequency distributions (Table V) are, therefore, expressed as percentages of the total number of variates. In this manner 49 pure type plants, 43 pure rogues, 69 F_1 hybrids, and 104 F_2 plants were measured.

The mean, standard deviation, and coefficient of variation of the ratios at each node and for the plant as a whole were calculated from the data in Table V. These statistical constants are given in Table VI. Figure 1 shows the graphs obtained by plotting the means for each node in each

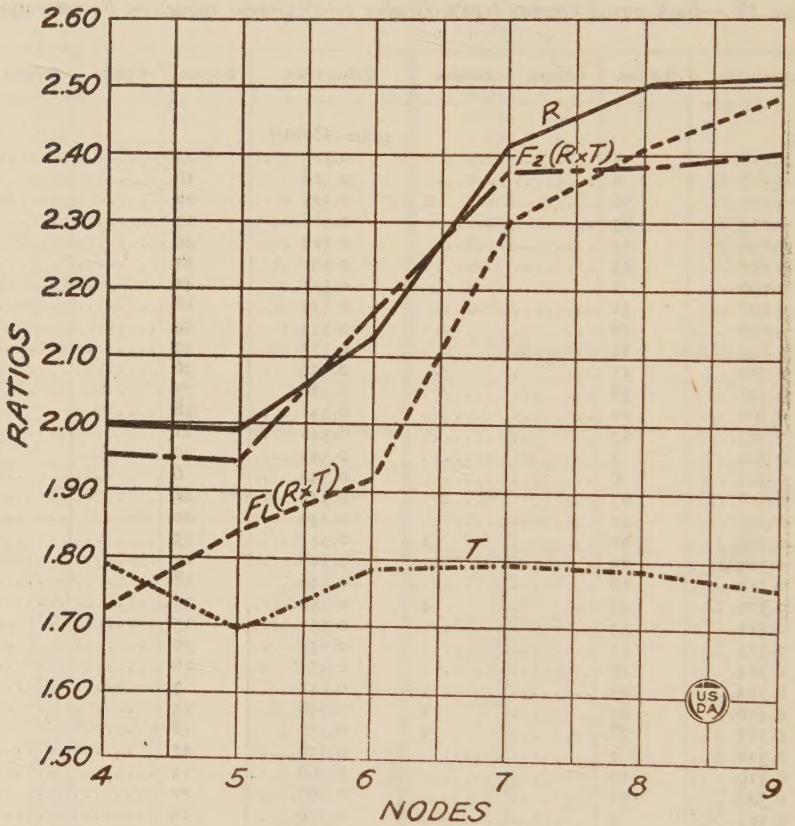

FIG. 1.—Graphs obtained by plotting the mean ratio of $\frac{\text{length of stipule}}{\text{width of stipule}}$ at the fourth to ninth nodes of Gradus type (T), Rogue (R), and the F_1 and F_2 hybrids of crosses between Gradus and Gradus-rogue, based on data from Table VI.

group of plants. The similarity of the F_1 and F_2 generations to the rogue parent is easily seen by inspection of Figure 1 and Tables V and VI. The F_1 hybrids up to the seventh node are like the type, or intermediate between the type and rogue; above the seventh node the plants become rapidly more roguelike. At all nodes the F_1 plants appear more variable than Gradus and are like the rogues in this respect.

TABLE V.—*Frequency distribution of ratio* $\left(\frac{\text{length of stipule}}{\text{width of stipule}}\right)$ *at the fourth to the ninth nodes in Gradus rogue, Gradus, F_1 and F_2 hybrid plants. As the number of stipules measured at each node was not always the same, the ratios in any one class are expressed in percentages*

Ratio.	Nodes.						
	Fourth.	Fifth.	Sixth.	Seventh.	Eighth.	Ninth.	Total.
Gradus rogue:	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
1.25	.....	.....	.....	.....	.....	.....	.....
1.35	.....	.....	3.02	3.02	.....	.....	0.45
1.45	2.66	1.20	.....	0	.....	.....	.67
1.55	5.32	2.40	1.16	0	.....	.....	1.56
1.65	10.64	6.00	1.16	1.51	.....	.....	3.36
1.75	13.30	8.40	3.48	0	.....	3.56	4.93
1.85	9.31	18.00	9.28	0	3.75	3.56	7.84
1.95	5.32	12.00	10.44	3.02	0	1.78	5.79
2.05	11.97	25.20	24.36	4.53	2.50	0	12.55
2.15	10.64	8.40	10.16	4.53	2.50	0	6.73
2.25	15.96	8.40	16.24	10.35	6.25	5.34	10.76
2.35	6.65	4.80	10.16	12.08	16.25	5.34	9.64
2.45	5.32	3.60	.48	21.14	12.50	1.24	9.42
2.55	1.33	1.20	4.64	16.61	21.25	28.44	11.21
2.65	0	.....	1.16	19.63	16.25	19.58	8.52
2.75	1.33	.....	0	3.02	10.00	8.90	3.58
2.85	.....	.....	1.16	.....	0	5.34	.89
2.95	.....	.....	.....	.....	6.25	1.78	1.34
3.05	.....	.....	.....	.....	1.25	1.78	.45
3.15	.....	.....	.....	.....	1.25	.....	.22
	[a] 75	[a] 83	[a] 86	[a] 66	[a] 80	[a] 56	.....
Gradus:							
1.25	.....	.....	.....	.....	.....	.....	.....
1.35	5.40	1.08	2.24	.....	.....	.....	1.59
1.45	6.48	3.24	3.36	6.18	1.08	.....	3.78
1.55	10.80	19.44	8.96	10.30	7.56	9.52	11.35
1.65	11.88	24.84	11.20	13.39	15.12	21.42	15.93
1.75	19.44	23.76	30.24	19.57	29.16	33.32	25.30
1.85	35.64	18.36	20.16	23.69	27.00	19.04	24.70
1.95	3.24	7.56	13.44	13.39	16.20	10.90	10.95
2.05	4.32	0	6.72	7.21	2.16	4.76	4.18
2.15	0	1.08	3.36	6.18	0	0	.20
2.25	0	0	0	0	0	0	0
2.35	1.08	.....	.....	.....	.....	.....	.02
2.45	.....	.....	.....	.....	.....	.....	.....
	[a] 91	[a] 92	[a] 89	[a] 97	[a] 91	[a] 42	.....
F_1 hybrid:							
1.25	.85	.....	1.46	.....	.....	.....	.41
1.35	.85	.75	0	.77	.....	.....	.41
1.45	5.10	1.50	1.46	0	.....	.....	1.38
1.55	16.15	10.50	1.46	.77	.....	.....	4.98
1.65	30.60	16.50	10.22	.77	.....	.....	10.11
1.75	22.10	16.50	10.95	.77	1.60	.....	9.14
1.85	22.10	19.50	20.44	4.62	1.60	.....	12.18
1.95	4.25	10.50	13.14	5.39	1.60	.....	6.37
2.05	3.40	18.75	12.41	10.01	8.80	1.35	8.44
2.15	0	12.00	9.49	11.55	3.20	1.35	5.67
2.25	.85	9.00	10.95	13.86	12.00	10.80	8.72
2.35	1.70	.75	3.65	17.71	12.00	20.25	8.44
2.45	.....	0	.73	8.47	17.60	18.90	6.65
2.55	.....	0	2.19	14.63	19.20	24.30	8.86
2.65	.....	.75	.73	6.16	10.40	14.85	4.71
2.75	.....	.....	.....	2.31	7.20	5.40	2.21
2.85	.....	.....	.....	1.54	.80	1.35	.55
2.95	.....	.....	.....	.....	3.20	1.35	.69
	[a] 117	[a] 132	[a] 136	[a] 129	[a] 124	[a] 74	.....

TABLE V.—*Frequency distribution of ratio* $\left(\frac{\text{length of stipule}}{\text{width of stipule}}\right)$ *at the fourth to the ninth nodes in Gradus rogue, Gradus F_1 and F_2, hybrid plants. As the number of stipules measured at each node was not always the same, the ratios in any one class are expressed in percentages*—Continued.

Ratio.	Nodes.						
	Fourth.	Fifth.	Sixth.	Seventh.	Eighth.	Ninth.	Total.
	Per cent.	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*	*Per cent.*
F_2 hybrid:							
1.05	.49	.....	.....	.....	.....	.....	.08
1.15	.96	.49	.....	.....	.....	.....	.24
1.25	.96	0	.....	.....	.....	.....	.16
1.35	.96	.49	.....	.....	.....	.....	.24
1.45	.48	.49	.....	.....	.....	.....	.16
1.55	1.45	.98	.....	.....	.....	.....	.41
1.65	6.26	3.42	.....	.....	.....	.....	1.62
1.75	11.20	14.20	.96	.....	.....	.....	4.37
1.85	15.80	22.42	4.33	1.44	.49	.49	7.52
1.95	14.50	20.42	3.85	1.44	.49	.49	6.87
2.05	26.10	21.40	27.40	4.82	4.90	2.94	14.63
2.15	8.20	6.34	21.61	8.18	8.78	5.88	9.70
2.25	8.67	3.42	11.52	16.33	17.55	15.70	13.90
2.35	1.45	3.90	5.30	26.40	20.00	25.00	14.70
2.45	.96	.49	2.88	14.90	17.55	22.10	10.20
2.55	.48	.49	.48	18.20	21.92	13.20	9.55
2.65	.96	0	.....	4.81	4.39	10.30	3.48
2.75	.48	.49	.....	2.40	3.42	2.40	1.53
2.85	.....	.....	.....	.96	.49	1.47	.48
	[a] 207	[a] 205	[a] 208	[a] 208	[a] 205	[a] 204	.....

[a] The actual number of measurements from which the frequency distributions (expressed in percentages) were derived.

TABLE VI.—*Constants for stipule shape calculated for each node separately and for the plant as a whole, based on data in Table V*

	Nodes.						
	Fourth.	Fifth.	Sixth.	Seventh.	Eighth.	Ninth.	All.
Type:							
M	1.705	1.706	1.782	1.797	1.782	1.766	1.765
σ	.205	.155	.170	.177	.130	.130	1.53
C. V.	12.05	8.11	9.55	9.88	7.30	7.32	8.66
Rogue:							
M	2.001	1.994	2.133	2.411	2.500	2.515	2.259
σ	.294	.223	.223	.288	.257	.266	.339
C. V.	14.70	11.20	10.46	11.53	10.28	10.59	15.00
F_1 hybrid:							
M	1.725	1.846	1.926	2.308	2.410	2.485	2.118
σ	.174	.217	.275	.266	.261	.172	.377
C. V.	10.11	11.79	14.32	11.56	10.82	6.93	17.79
F_2 hybrid:							
M	1.957	1.941	2.173	2.370	2.384	2.405	2.205
σ	.256	.206	.148	.184	.170	.171	.275
C. V.	13.08	10.61	6.81	7.75	7.13	7.71	12.47

The F_2 hybrids differ from the F_1 generation in being remarkably like the pure rogues at all stages in their development. The stipules at the fourth, fifth, and sixth nodes of the former are especially different from those of the F_1 plants. The measurements serve to emphasize what is plainly seen by inspection of the cultures, namely, that the F_2 seedlings resemble the pure rogues of the same age rather than the young F_1 plants which so generally exhibit a typelike character. To the eye, neither of the hybrid generations, at maturity, differs in any appreciable way from the rogue parent.

Besides measuring the stipules at the fourth to the ninth nodes in the case of the rogue, type, and F_1 and F_2 hybrids, measurements were made of four stipules per plant from about the eighth to the fourteenth node of mature individuals in each category. The mature plants measured included those used in the comparison by nodes of the four groups, and, in the case of all but the F_1 hybrids, additional plants were measured.

In Table VII are shown the frequency distributions and statistical constants calculated for each of the four categories of plants. The range of variation is strikingly significant, the range of the type not overlapping that of the rogue. The F_1 and F_2 hybrids have a range of variation equal in extent to that of the rogue parent. The F_2 generation differs from the pure rogue and the F_1 in that it is less variable as indicated by the coefficients of variation (Coefficient Variation): F_2 generation, 5.84 ± 0.2677; rogue, 7.06 ± 0.2912; F_1 generation, 7.09 ± 0.3662, respectively. The probable errors of the differences between the coefficients of variation of the pure rogue and of the F_2, and of the F_2 and F_1, are practically three times the difference, in each case indicating that the differences are real. However, the differences in variability of the three groups as shown by the stipule measurements of the mature plant were not apparent on inspection of the cultures.

The resemblance of the F_1 and F_2 hybrids to the pure rogues is further accentuated by a comparison of the mean stipule ratio of the three. The mean for the rogue parent is 2.339 ± 0.0096; for the F_1, 2.383 ± 0.0196; and for the F_2 it is 2.360 ± 0.0089. There is no significant difference between any of the three means.

Thus in regard to variability, range of variation, and mean stipule ratio, the two hybrid generations resemble only the rogue parent. The influence of the type parent, in crosses between type and rogue is apparent only in the F_1 plant and at only the lower nodes.

CROSSES BETWEEN THE GRADUS STRAIN AND MUMMY, A NONROGUE-PRODUCING VARIETY.

In 1918 the English "Mummy" pea was used in crosses with Gradus rogue and Gradus type. Seed of the Mummy variety was first obtained from O. E. White of the Brooklyn Botanical Garden (White's No. P1–3–4–2), and only this strain has been used in the crosses. In Mummy, fasciation of the main stem is characteristic, but does not appear until the plant is well developed. With the appearance of the fasciated condition the stipules become narrower and more pointed than those at the lower and middle nodes of the same plant. Plate 2, A, B, C is of a mature plant of Mummy. Although having stipules much narrower than in Gradus type, no rogue comparable to those found in Gradus have ever been observed by the writer among the several thousand

TABLE VII.—*Frequency distributions and statistical constants of ratio of* $\frac{\text{length of stipule}}{\text{width of stipule}}$ *for Gradus type, Gradus rogue, P 16, and of the F_1 and F_2 generations of various hybrids and hybrid segregates from crosses between the three parent types. The frequency distributions and statistical constants for the F_2 generation of Gradus rogue×Mummy are based on data in Table XIV.*

Types, hybrids and segregates.	1.35	1.45	1.55	1.65	1.75	1.85	1.95	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	3.05	Total.	M	σ	Coefficient variation.
Gradus type (P_1)	1	0	16	64	33	18	3												135	1.693±0.0107	0.098±0.0075	5.78±0.2381
Gradus rogue (P_{16})								7	21	33	30	22	10	8	4				135	2.339± .0096	.165± .0068	7.06± .2912
Gradus type×Gradus rogue (F_1)								6	4	18	23	12	11	10	2				86	2.383± .0196	.169± .0087	7.09± .3662
Gradus type×Gradus rogue (F_2)								4	3	33	30	23	10	5	1				109	2.360± .0089	.138± .0063	5.84± .2677
Mummy (P_{11})						3	29	68	56	15	5								176	2.088± .0050	.100± .0073	4.77± .1719
Gradus type×Mummy (F_2), all		1	1	7	21	19	24	8	2	1	2								87	1.868± .0115	.159± .0081	8.51± .4382
AA and *Aa* segregates (colored)				3	12	15	11	8	2	0	2								53	1.905± .0142	.154± .0101	8.08± .5394
A, B, C, segregates (purple)				2	9	10	8	6	2	0	2								39	1.909± .0175	.162± .0124	8.48± .6523
A, B, segregates (pink)				1	3	5	3	2											14	1.864± .1950	.112± .0136	6.00± .7415
aa, segregates (white)	1	1	4	6	3	6	0	0	1										22	1.710± .0260	.181± .0184	10.58±1.0873
Gradus rogue×Mummy (F_2) all		1	11	37	86	143	167	122	136	187	231	169	131	58	39	12	4		1,534	2.307± .0049	.288± .0035	12.48± .1542
AA, Aa, segregates (colored)			4	18	52	107	133	88	100	152	181	142	107	46	33	11	4		1,178	2.326± .0016	.281± .0011	12.08± .0475
A, B, C, segregates (purple)			4	12	40	79	95	66	78	118	132	106	79	29	24	9	2		873	2.323± .0063	.278± .0045	11.95± .1805
A, B, c, segregates (pink)				6	12	28	38	22	22	34	49	36	28	17	9	2	2		305	2.336± .0110	.286± .0078	12.24± .3392
aa, segregates (white)		1	7	19	34	36	34	34	36	35	50	27	24	12	6	1			356	2.230± .0106	.297± .0075	13.31± .3338
Gradus rogue×Mummy (F_2) all (omitting Nos. 0.1059 and 0.1093)		1	8	30	72	102	122	110	133	183	230	169	131	58	39	12	4		1,404	2.333± .0050	.280± .0036	12.00± .1549
AA and *Aa,* segregates (colored)			3	16	45	74	94	77	97	148	180	142	107	46	33	11	4		1,077	2.355± .0056	.275± .0039	11.67± .1720
A, B, C, segregates (purple)			3	12	37	58	64	60	75	115	132	106	79	29	24	9	2		805	2.349± .0064	.271± .0045	11.53± .1964
A, B, c, segregates (pink)				4	8	16	30	17	22	33	48	36	28	17	9	2	2		272	2.375± .0110	.269± .0078	11.32± .3427
aa, segregates (white)		1	5	14	27	28	28	33	36	35	50	27	24	12	6	1			327	2.258± .0110	.294± .0077	13.02± .3491
Gradus rogue×Mummy (F_2) all (Nos. 0.1059 and 0.1093)			3	7	14	41	45	12	3	4	1								130	1.998± .0082	.139± .0058	6.95± .2912
AA and *Aa* segregates (colored)			1	2	7	33	39	11	3	4	1								101	2.027± .0087	.127± .0060	6.26± .2982
A, B, C, segregates (purple)			1	0	3	21	31	6	3	3									68	2.038± .0095	.116± .0067	5.69± .3290
A, B, c, segregates (pink)				2	4	12	8	5	0	1	1								33	2.008± .0170	.145± .0120	7.22± .6025
aa, segregates (white)			2	5	7	8	6	1											29	1.899± .0159	.127± .0112	6.68± .5899

plants of Mummy grown in the last three years. The Mummy variety differs from Gradus in several Mendelian characters.

NOMENCLATURE.—The factors concerned in the crosses of Mummy and Gradus and the symbols used to designate the factors are as follows:

A. Factor for flower color. A must be present to have any color develop. Alone A produces light purple flowers; a produces white flowers. Dominance is complete. Tedin, (*11*).
B. Interacts with A to produce pink flowers; b has no visible effect. Tedin, (*11*).
C. Interacts with A to produce violet flowers. Interacts with AB to produce dark purple; c has no visible effect on A or B. Tedin, (*11*).
N. Factor for normal stem as opposed to n for fasciated. Mendel, (*8*); White, (*14*).
X. Factor for mean stipule ratio of approximately 2.35. The allelomorph x in Gradus determines a ratio of about 1.70. (Described here.)
x′. Factor for stipule shape in Mummy allelomorphic to X in Gradus rogue and x in Gradus.
Y. Factor responsible in Mummy for mean stipule ratio of approximately 2.05. Its allelomorphy in Gradus determines a stipule ratio of about 1.70. (Described here.)

It is tentatively assumed that the change which takes place when Gradus produces Rogue is a point mutation of factor x to X.

To find the mean stipule ratios for which it is assumed Xx and Yy are responsible, the average ratio of width to length was obtained for four stipules from the middle nodes of each plant measured. In this manner the mean stipule ratio per plant was obtained for 135 Gradus types, 135 Gradus rogues, and 176 plants of the Mummy variety. Frequency distributions of the three groups of mean ratios were made (Table VII) and the mean, standard deviation, and coefficient of variation calculated for each category of plants. The mean stipule ratios were found to be: Gradus type 1.693 ± 0.0107; Gradus rogue, 2.339 ± 0.0096; and Mummy, 2.088 ± 0.0050.

In regard to the factors here considered, the three strains have the following genetic constitution:

Gradus type, aaBBCCxxyyNN.
Gradus rogue, aaBBCCXXyyNN.
Mummy, AABBccx′x′YYnn.

GRADUS TYPE × MUMMY

RELATION OF THE X AND X′ FACTORS FOR STIPULE WIDTH

From the data at hand, factors x and x′ are considered to have practically the same somatic expression in regard to stipule shape. The difference is in the ability of x to mutate to X, a quality lacking in x′, at least in the x′x′ or xx′ combination. In other respects the two allelomorphic factors x and x′ can be viewed as essentially indentical, as far as visible expression is concerned.

RELATION OF COLOR FACTORS A AND a

Considering the allelomorphic pair A and a in the F_2 generation of crosses of Gradus type with Mummy, the colored flowered plants (AA and Aa) and noncolored (aa) are found to be in close agreement with the expected 75 and 25 per cent (Table VIII).

TABLE VIII.—*Gradus×Mummy and Gradus rogue×Mummy in the F_2 generation (aa×AA)*

TYPE×MUMMY

	AA, Aa.	aa.	Total.
Observed	563	179	[a] 742
Percentage found	75.88	24.12	.....
Percentage expected	75.00	25.00	.....
Difference (D)	0.88	0.88	.....
Standard error (S. E.)	1.17	.....	.....
D/S. E	0.75	.....	.....

ROGUE×MUMMY

Observed	1178	356	1,534
Percentage found	76.79	23.21	.....
Percentage expected	75.00	25.00	.....
Difference (D)	1.79	1.79	.....
Standard error (S. E.)	.74	.....	.....
D/S. E	2.41	.....	.....

[a] Data from 25 F_2 families including 2 families (34 plants) classified as to color segregation and measured for ratio of width to length of stipule but not classified as to stipule shape, i. e., as types or intermediates.

RELATION OF COLOR FACTORS A AND C

The F_1 plants of Gradus type×Mummy were all purple-flowered. The F_2 generation gave the expected recombinations in approximately the proportion 56.25 per cent purple (with factors A, B, and C), 18.75 per cent pink (with factors A and B), and 25.00 per cent white (with factors aa), the observed number in each class being in sufficient agreement with that theoretically expected when two factors are independently inherited (Table IX).

TABLE IX.—*Segregation of factors for flower color in F_2 generation of cross Gradus with Mummy and of Gradus rogue with Mummy (aaBBCC×AABBcc)*

GRADUS×MUMMY

	Purple ABC.	Pink ABc.	White aBc, aBC.	Total.
Observed	406	157	179	742
Percentage found	54.72	21.16	24.12	.....
Percentage expected	56.25	18.75	25.00	.....
Difference	1.53	2.41	.88	.....
χ^2=2.8854.				
P=.3405.				

GRADUS ROGUE×MUMMY

Observed	873	305	356	1,534
Percentage found	56.91	19.88	23.21	.....
Percentage expected	56.25	18.75	25.00	.....
Difference	.66	1.13	1.79	.....
χ^2=3.0225.				
P=0.2214.				

From seeds of 25 F_1 hybrids, 742 F_2 hybrids were matured in 1920. A total of 708 individuals, belonging to 23 families, were classified according to stipule shape as Graduslike types (yy) and intermediates (YY or yy), the latter class being made up of plants resembling Mummy in stipule character. The remaining families, consisting of 34 plants, were not directly classified in the same way, but the mean stipule ratio per plant was calculated from measurements of the width and length of the stipules. A record of the flower color was kept for all the 742 F_2 plants (Tables VIII and IX).

Of the 708 plants classified according to stipule shape, 540 were grouped as intermediates resembling Mummy and 168 as Graduslike types (Table X), indicating a single factor difference, in regard to stipule shape, between Gradus type and Mummy. The expected percentage in the two groups is 75 per cent intermediates and 25 per cent types; the observed percentages, 76.27 per cent intermediates and 23.73 per cent Graduslike types, in the F_2, are well within the limits of the standard error. The standard error as used here is calculated according to the formula of Yule (*16*).

TABLE X.—*Segregation of stipule shape in F_2 generation of Gradus×Mummy* (yy×YY)

GRADUS×MUMMY

	YY, Yy	yy	Total.
Observed	540	168	708
Percentage found	76.27	23.73	.....
Percentage expected	75.00	25.00	.....
Difference (D)	1.27	1.27	.....
Standard error (S. E.)	1.09	.....	.....
D/S.E.	1.16	.....	.....

RELATION OF Y AND y, FACTORS FOR STIPULE SHAPE

In all, 37 F_1 plants were grown in 1919 from the cross Gradus type with Mummy. In size and shape the stipules of the F_1 plants were intermediate between Mummy and Gradus type. The upper part of a branch of a mature F_1 plant is shown in Plate 3, A.

LINKAGE RELATION OF Yy AND Aa

The relation of the factor pairs Yy and Aa was determined from a count of 708 F_2 plants of the cross Gradus type with Mummy (aayy×AAYY). In Table XI are tabulated the observed numbers of the F_2 recombinations. The actual ratios of the four classes AY, aY, Ay, and ay indicate that factors AY and ay are linked. The calculated zygotic series is approximately 66 AY : 9 Ay : 9 aY : 16 ay; the gametic series approximately 4 : 1 : : 1 : 4; and the percentage of crossing-over for all the F_2 families is 20.41 ± 1.28 per cent, using Haldane's method (*6*) for the determining of zygotic and gametic series from observed F_2 frequencies.

TABLE XI.—*Linkage relation of* Aa *and* Yy *from F_2 generation of Mummy×Gradus*

	aayy×AAYY.				
	AY.	Ay.	aY.	ay.	Total.
Observed	476	63	64	105	708
Calculated	467	64	64	113	.....
Difference	9	1	0	8	.....
$\chi^2 = 0.7554$	.....	.....	.....	.....	.....

Plates 4 A, B, and 5 A, B, are of the upper parts of a Graduslike type and of an intermediate segregate, respectively, from the F_2 of Gradus × Mummy. The intermediate shown has stipules wider than the stipules of the F_1 plant of the same cross shown in Plate 3, A. The difference is largely due to the fact that the stipules of the F_1 plant are on a branch while those of the F_2 intermediate are on the main stem. Stipules on a branch are smaller and narrower than those of the main stem in nearly all instances, irrespective of the variety or strain.

It should be pointed out here that Y and y are considered as the factors chiefly responsible for the difference for stipule shape between Mummy and Gradus. It is highly probable, from the increased variability of the F_2 generation over that of the parents, that a number of modifying factors interact with Y and y to affect stipule shape.

RELATION OF FACTORS Aa FOR FLOWER COLOR AND Nn FOR CHARACTER OF STEM

It has been said before that stipules from the fasciated portion of the stem of Mummy are narrower than those of the apparently nonfasciated part of the same plant or from a normal plant. The F_1 plants of the crosses of Mummy with Gradus were normal stemmed and had narrow, intermediate, or Mummylike stipules. No accurate counts were made of the fasciated F_2 segregates, but apparently the expected 3 : 1 ratio of normal to fasciated plants occurred.

Since fasciated plants appeared, on the whole, to have narrower stipules than normal plants, it might be suggested that linkage existed between n and A, and N and a, so that the existence of a factor pair Yy would not have to be assumed. That such is not the case is shown by the results of White (*14*), who found factors Aa and Nn to be independently inherited. The two cases are comparable as the AAnn parent of the hybrids studied by White was from the same strain as that used by the present writer.

STATISTICAL EVIDENCE OF LINKAGE BETWEEN FACTORS AY AND ay

In addition to the stipule measurements of the 34 plants mentioned in the preceding section, stipules of 41 other plants were measured from the F_2 generation of Gradus × Mummy. Of the 75 plants measured (Table VII), 53 were A segregates (39 purples and 14 pinks) and 23 were a segregates (whites). The mean stipule ratio of the F_2 plants as a whole was found to be 1.868 ± 0.0126, for the A's 1.905 ± 0.0142, and for the a's 1.710 ± 0.0260. Considering a difference between the means of at least three times the probable error of the difference as being significant, it is found that the difference between the means of the A and a segregates is significant, since it is five times the standard error.

The same relation holds between the mean ratio of the colored and white F_2 segregates, whether the A plants be considered collectively, or separately as purples (with the factors A and B) and as pinks (with the factors A and b), the mean of the purples being 1.909 ± 0.0175 and of the pinks 1.864 ± 0.0142 as compared with 1.905 ± 0.0142 for the A segregate as a whole (Table VII).

No essential difference exists between the means of Gradus and the white-flowered (aa) F_2 segregates from the cross Mummy with Gradus. However, the hybrid whites show a greater variability than do the pure whites, the coefficient of variation of the former being 10.58 ± 1.0870 compared with 5.78 ± 0.2381 for the latter.

The increased variation of the F_2 aa plants is probably due for the most part to crossing-over of the factors Yy for stipule shape and partly to the recombination of modifying factors affecting the same character.

The mean ratio of the A segregates, 1.905 ± 0.0142, is significantly less than that of the Mummy parent, 2.088 ± 0.0050, and the variability of the former is greater than that of the pure AA plants. The increased variability of the colored-flowering segregates, besides being accounted for largely by crossing-over, could, in addition, be due to a dissimilarity in stipule shape of AA and Aa plants. The heterozygous plants being in excess would tend to lower the mean of the population. Actually the F_1 plants did appear to have stipules intermediate in shape between those of the two parents, but no measurements are available for comparison.

It is realized that the number of F_2 individuals measured is small but, taken alone, the statistical results would offer fairly good evidence of linkage between the factor or factors for stipule shape and the A factor for flower color. In connection with the F_2 classification based on stipule shape and flower color, the fact of linkage between the Aa and Yy factors is well established.

GRADUS ROGUE × MUMMY

The Gradus rogues used in the series of crosses with Mummy were all descended from a rogue plant, S15, selected in 1916 from a commercial planting of Gradus. Progeny of the same rogue, S15, when crossed with Gradus type behaved as typical rogues in inheritance (cultures 9.1270–9.1275, 9.1320, and 9.1321, Table II).

The F_1 plants (Table XII) of Gradus rogue × Mummy, and reciprocal had, with one exception, rogue stipules, and in this respect appeared similar to the pure rogues. As volunteer crossing occurred in the F_1 of Gradus rogue × Gradus, it might be expected to take place among the F_1 hybrids of rogue and Mummy. Since the F_1 plants in the latter cross exhibited most of the dominant Mendelian factors present in any of the strains growing in the experimental gardens in 1919, it would be difficult to detect volunteer hybrids in the F_2 generation (F_1 out-crosses). However, as the F_1 hybrids were very late in flowering, cross-pollination by insects, if not entirely absent was cut down to a minimum.

TABLE XII.—*Pedigrees of F_1 cultures of Gradus rogue × Mummy (P16) and reciprocal*

Culture.	Pedigree.	Mature plants.
9.720	(S15–2–5r x P16–10)—1 to 6	Rogues.
9.721	(S15–2–12r x P16–10)—1 to 9	Do.
9.722	(S15–2–3r x P16–10)—1 to 7	Do.
9.723	(S15–2–19r x P16–10)—1 to 6	Do.
9.725	(S15–1–6r x P16–10)—1 to 3	Do.
9.726	(S15–1–9r x P16–10)—1 to 8	Do.
9.727	(S15–3–11r x P16–10)—1 to 8	All rogues but No. 6, which resembled F_1 of P 16 x type.
9.728	(S15–3–4r x P16–10)—1 to 3	Rogues.
9.729	(S15–3–5r x P16–10)—1 to 8	Do.
9.730	(P16–12 x S15–4–5r)—1 to 11	Do.
	Total 69	

As some uncontrolled pollinations may have occurred, there is possibly an experimental error in the results which should be kept in mind when interpreting the F_2 data. On this account the crosses are being repeated, and it is planned to grow the F_1 generation under glass for protection. It is believed, however, that the data here presented are of sufficient interest to warrant publication at this time and that the errors from out-crossing will prove minimal.

RELATION OF THE A AND A FACTORS FOR FLOWER COLOR

The F_1 plants of the crosses between rogue and Mummy had colored (purple) flowers. In Table VIII is shown the percentage of colored-flowered (AA + Aa), segregates to white-flowered (aa), segregates in the F_2 generation of rogue × Mummy, and reciprocal. The observed percentages, 76.79 per cent AA and Aa plants and 23.21 per cent aa segregates conform to expectation.

RELATION OF A AND C, FACTORS FOR FLOWER COLOR

Gradus rogue × Mummy in the F_2 generation gave approximately the expected 56.25 per cent purples (with factors A, B, and C); 18.75 per cent pinks (with factors A and B); and 25.00 per cent whites (with factors aa), the observed percentages being 56.91 per cent, 19.88 per cent and 23.21 per cent, respectively, the deviations being well within the limits of error due to random sampling (Table IX).

Although the dovetailing of observation and theory is good for the three classes of color segregates as a whole, there is in the F_2 in both the case of Mummy × Gradus and Mummy × Gradus rogue, a deficiency of white segregates. The deficiency of aa plants can be explained by differences in disease resistance as well as by variations in time of maturing between colored and noncolored F_2 segregates. On the whole, plants with colored flowers are more resistant to disease than are the white flowered forms, so that proportionately more of the latter would be lost before they reached maturity. For unavoidable reasons the F_2 data were collected late in the season after a number of the plants had matured. Plants whose stipules were too dried to measure were not classified as to flower color but their occurrence was noted. Tschermak (*12*), Hoshino (7), and others have noted a correlation between the presence of the A factor and the habit of late flowering. In all probability the same correlation existed in these cultures. On this account, relatively more of the white segregates than of the colored ones were too mature to be used in this study at the time the stipule measurements were made.

RELATION OF N AND N FACTORS FOR NORMAL AND FASCIATED STEM, RESPECTIVELY

The 69 F_1 plants of Gradus rogue × Mummy had normal stems. No F_2 counts were made of the normal and fasciated plants, but apparently there occurred the expected Mendelian segregation.

RELATION OF Xx′ AND Yy FACTORS FOR STIPULE SHAPE

In 1919, 69 F_1 hybrids (Table XII) were grown from the seed of 13 pollinations made the preceding year. The young plants resembled Mummy in regard to stipule shape and were uniform in appearance.

With the exception of one plant (9.727–6), the hybrids were all classified as rogues at maturity. Plate 3, B, is of the upper part of a branch of a mature F_1 plant from Mummy × Gradus rogue.

The exceptional plant (9.727–6) resembled the F_1 of Mummy × Gradus, although 7 other plants from the same cross had rogue stipules. The atypical F_1 hybrid (9.727–6) produced 61 F_2 plants in 1920 (Culture No. 0.1084). At the time the notes were taken 14 individuals were too dried to classify. Of the 47 remaining plants, 23 were grouped as intermediates, with stipules intermediate in shape between those of Mummy and those of Gradus, and 24 were classed as Graduslike types. Apparently there were no rogues among the F_2 offspring.

Besides the F_2 family (0.1084) derived from the atypical F_1 plant, five other F_2 cultures were classified by inspection as rogues and nonrogues, the latter being subdivided into broads and intermediates (Tables XIII and XIV). The number of individuals in each of the three categories is shown in Table XIV. The ratio of rogues to nonrogues indicates a single factor difference between the two parents as being primarily responsible for the difference in stipule shape. The observed ratio of 77.12 per cent rogues to 22.88 per cent nonrogues agrees with that theoretically expected being within the error due to the limitations of random sampling.

On the assumption of a single factor pair, X and x′, primarily responsible for a difference in mean stipule ratio of 2.05 in Mummy and as compared with 2.35 in Gradus rogue, one would expect the F_2 to segregate only into rogues and Mummylike plants. Actually three classes based on stipule shape were distinguished, namely, rogues, intermediates (Mummylike), and broads (Table XIV), the latter having stipules comparable to those of Gradus.

TABLE XIII.—*Classification into rogues and nonrogues of five F_2 families from the cross Gradus rogue × Mummy*

Parent.	Culture No.	Rogues.	Nonrogues.		Unclassified.	Total.
			Intermediate.	Broad.		
1919:	1920:					
9.726–5	0.1076	79	19	3	8	109
9.726–6	0.1077	68	15	2	1	86
9.726–7	0.1078	8	4	2	2	16
9.726–8	0.1079	11	4	0	4	19
9.727–8	0.1085	16	4	1	6	27
		182	46	8	21	257

TABLE XIV.—*Relation of Xx′ and Yy in F_2 generation of cross Mummy×Gradus rogue (x′x′ YY × XXyy), data from Table XIII.*

	XY or Xy rogues.	x′Y or x′y nonrogues.		Total.
		Intermediate.	Broads.	
Observed, 12:3:1 ratio	182	46	8	236
Percentage found	77.12	19.49	3.39	.....
Percentage expected	75.00	18.75	6.25	.....
Difference (D)	2.12	.74	2.86	.....
χ^2=2.8587				
P=.2231				
Observed, 3:1 ratio	182	54	.....	236
Percentage found	77.12	22.88	.....	.....
Percentage expected	75.00	25.00	.....	.....
Difference (D)	2.12	2.12	.....	.....
Standard error (S. E.)	1.89	.....	.....	.....
D/S. E.	1.12	.....	.....	.....

The presence of the broads in the F_2 generation of the cross Gradus rogue with Mummy is accounted for by assuming the presence of two factors y and x for stipule width in Gradus, factor y being allelomorphic to Y in Mummy and factor x allelomorphic to x′ found in Mummy. Ordinarily neither x nor x′ has any visible effect on stipule shape in either variety. Occasionally the factor x in Gradus mutates to X, which has for its somatic expression a mean stipule ratio of about 2.35. Factor X interacts with its allelomorph x as found in Gradus and is dominant to x′ of Mummy. It also masks either member of the factor pair Yy. Any F_2 segregate that is heterozygous or homozygous for the factor X has rogue stipules, irrespective of whether Y or y is present. An individual in which X is absent has intermediate or broad stipules, depending on the presence or absence, respectively, of the factor Y. In the F_2 generation the plants segregate into approximately 12 rogues; 3 intermediates; 1 broad, according to the following scheme:

P_1 ..... Gradus rogue, XXvy×Mummy, XX x′ x′
F_1 ..... Rogue, Xx′ Yy

F_2	Rogues:			Intermediates:		Broads:
	Xy	Xy		x′Y		x′y
Percentage	56.25	18.75		18.75		6.25
Ratio	12		:	3	:	1

	Rogues (X):	Non-rogues (X′):
Percentage	75	25
Ratio	3	: 1

	Rogues and Intermediates:	Broads:
Percentage	93.75	6.25
Ratio	15	: 1

Returning again to the results tabulated in Table XIV, the observed number in any one category of plants is expressed in percentages of the total number of plants classified. For the rogues, intermediates, and types the percentages are 77.12, 19.49, and 3.39, respectively, compared with the theoretically expected 75.00, 18.75, and 6.25 for the respective classes, the deviations of the observed percentages from the calculated are not statistically significant (P having a value of 0.2331). The greatest deviation is caused by the exceptionally low number of board-stipuled plants found. The deficiency in the broad class, however,

may be partially explained by assuming a differential mortality rate among the F_2 segregates as explained in the paragraph dealing with the relation of the Aa and Cc factors in the F_2 generation of Gradus rogue × Mummy.

The occurrence of the early flowering segregates offers a partial explanation of the deviation in the number of broad-stipuled plants observed from that theoretically expected, as there is in all likelihood a correlation in Gradus and Mummy between the shape of the stipules and time of maturing. As has been shown, the Graduslike character of the broad-stipuled F_2 plants was inherited through the rogue parent, which also carried the factors for early flowering. The results with Gradus × Mummy show that linkage exists in Gradus between the factors y for stipule shape and a for flower color. Hoshino (7) has shown the factor a to be linked with a factor for early flowering. Necessarily linkage exists in some degree between the factor y for stipule shape and the factor for early flowering. One is, therefore, justified in assuming that many of the white, broad-stipuled segregates would be early in maturing and the correlation would account for a part of the deviation of the observed number of broad F_2 types from the number theoretically expected.

STATISTICAL STUDY OF THE F_2 GENERATION OF THE CROSSES GRADUS ROGUE AND MUMMY

In 1920 were grown 51 F_2 families of the cross Gradus rogue with Mummy. The average ratio of stipule width to length in the mature F_2 plants was calculated in the same manner as for the P_1 generation. The F_2 segregates were also classified according to flower color but not described as broads, intermediates, or rogues.

RELATION OF COLOR FACTORS A AND a TO STIPULATE SHAPE IN TWO ATYPICAL FAMILIES

With the exception of the plant already mentioned,[5] all of the F_1 hybrids were rogues and appeared similar in regard to stipule shape. Although somatically alike the F_2 frequency distributions of the progeny of two apparently normal F_1 rogues are different from those of the remaining 49 F_2 families in both their range of variation and mean stipule ratio (Table XV). The means of the two families are 1.999 ± 0.9106 and 1.905 ± 0.0126 and for the two together the mean is 1.998 ± 0.0082 as compared with 2.333 ± 0.0050 for the other 49 F_2 cultures (Table XVI).

Because of their similarity both in frequency distribution and in the value of the mean stipule ratios, the two anomalous cultures have been lumped together for a statistical study of the color segregates. The means of the three color classes are: For the whites, 1.899 ± 0.0159; for the pinks, 2.046 ± 0.0167; for the purples, 2.038 ± 0.0095; and for colored plants as a whole, 2.027 ± 0.0085. The difference in means of the AA and aa as compared with aa plants is 6.7 times the probable error. The frequency distribution of the a plants resembles more that of Gradus than it does that of Mummy or Gradus rogue. The frequency distribution of the A population resembles that of Mummy rather than that of either Gradus or Gradus rogue. The difference in the mean stipule ratios of the two color groups, as well as the difference in their ranges

[5] The two exceptional F_2 families were cultures numbered 0.1059 and 0.1093 (Table XV), the progeny of F_1 plants 9.722–1 and 9.729–5, respectively (Table XII).

TABLE XV.—*Gradus rogue × Mummy, and reciprocal. Frequency distributions of ratio of* $\left(\frac{\text{length of stipule}}{\text{width of stipule}}\right)$ *of* F_2 *families*

Culture No.	1.55	1.65	1.75	1.85	1.95	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	3.05	Total.	M.	Coefficient variation.
0.1045		1	0	1	4	4	3	1	5	7	2	3	2	2			35	2.325±0.0329	12.43±0.9848
0.1046		1	1	1	0	0	3	4	3	6	3	1					23	2.245± .0374	11.85±1.1949
0.1047					1	1	0	0	3	3	1	1	0	0	0	1	11	2.359± .0390	8.14±1.6217
0.1048			1	1	1	3	4	4	7	7	11	12	3	3	1	1	59	2.466± .0231	10.75± .6751
0.1049			1	0	2	5	4	5	2	7	6	8	3	0	0	1	44	2.396± .0850	11.48± .0850
0.1050			1	1	4	1	2	5	9	9	2	3	2	1			40	2.340± .0264	10.59± .8075
0.1051			1	5	2	6	6	5	10	8	4	3	2	1			53	2.283± .0245	11.56± .7674
0.1052					2	2	0	1	1	4	1	2	1				14	2.358± .0467	10.98±1.4190
0.1053			1	1	2	1	0	1	0	1							7	2.036± .0568	10.95±1.9973
0.1054		1	1	3	4	3	3	5	6	5	11	9	2	4	3		60	2.410± .0209	9.95±1.8113
0.1055				1	2	3	3	4	4	5	4	1	2				29	2.326± .0295	10.14± .9072
0.1056		1	1	5	3	7	9	6	6	17	6	8	1	2			72	2.312± .0215	11.72± .6580
0.1057			1	1	1	9	5	1	2	5	1	0	2				28	2.215± .0312	11.06±1.0033
0.1058						2	0	2	2	2	1	1					10	2.340± .0397	7.94±1.2142
0.1059 [a]		1	3	9	23	24	6	3	2								71	1.999± .0106	6.65± .3781
0.1060						1	0	0	2	1	1						5	2.350± .0494	6.97±1.5003
0.1061			2	0	3	3	1	0	1								10	2.000± .0358	8.40±1.2758
0.1062			1	2	1	1	2	1	3	4	6	1	1	2			25	2.370± .0362	11.35±1.0966
0.1063			1	1	0	1	1	1	2	4	1						12	2.160± .0522	12.41±1.7348
0.1064				1	1	0	2	4	4								12	2.208± .0302	7.02± .9684
0.1065	1	0	1	5	5	1	7	9	7	7	4	2	0	3			52	2.255± .0265	12.59± .8459
0.1066			1	1	3	1	1	3	4	3	3	3	1				24	2.312± .0370	11.63±1.1492
0.1067			1	1	5	5	6	7	3	7	9	8	5				57	2.357± .0256	12.17± .7798
0.1068		1	1	2	3	2	4	1	2	4	10	7	1	2			40	2.357± .0322	12.81± .9817
0.1069			2	3	4	6											15	2.215± .0313	12.59±1.0165
0.1070				1	1	0	2	2	1	1							8	2.175± .0436	8.41±1.4282
0.1071				2	0	2	3	1	4	0	4	1	2				19	2.328± .0414	11.51±1.2760
0.1072							1	2	2	4	0	0	1				10	2.390± .0334	6.65± .9998
0.1073					1	0	0	0	2	2							5	2.310± .0552	7.92±1.6998
0.1074			1	2	3	6	2	6	2	12	4	2	1				41	2.309± .0248	10.22± .7691
0.1075						4	0	1	1	4	2	0	2				14	2.372± .0386	9.02±1.1563
0.1080				1	0	0	2	1	4	2	0	1	0	1	1		13	2.397± .0525	11.72±1.5715
0.1081								2	3	1	3	2	1	0	2		14	2.543± .0398	8.69±1.1160
0.1082					3	4	1	2	4	11	5	8	2	2			42	2.434± .0251	9.90± .7356
0.1083				1	1	2	1	2	6	8	7	7	3	1	0	1	40	2.470± .0254	9.63± .7329
0.1086				1	0	2	0	1	1	1	1	2					9	2.317± .0607	11.65±1.8772
0.1087			2	0	0	2	3	1	3	1	1	3	2	1			19	2.350± .0479	13.19±1.4682
0.1088						3	0	0	4	4	2	3	1	1	1		19	2.472± .0385	10.07±1.1050
0.1089			2	2	6	2	5	6	7	11	10	3	3	2	1		60	2.350± .0245	11.91±1.4496
0.1090				3	5	1	1	4	6	5	6	2	0	1			34	2.303± .0304	11.41± .9453
0.1091			1	0	2	1	2	1	5	1	1	1					15	2.250± .0466	10.35±1.2893
0.1092				1	0	1	1	0	1	1							5	2.170± .0643	9.81±2.1125

O. 1093 [a]	.....	1	2	4	5	18	21	6	0	2	1	.....	.....	.....	.....	.....	.....	.....	59	1.905± .0129	7.72± .4822
O. 1094	.....		2	2	11	15	5	3	0	4	2	4	4	1	.....	.....	.....	.....	53	2.094± .0224	11.55± .7667
O. 1095	.....		1	0	3	4	6	4	13	12	18	5	3	1	1	.....	.....	.....	71	2.306± .0173	9.36± .5338
O. 1096	.....						2	0	0	0	2	.....	.....	.....	.....	.....	.....	.....	4	2.250± .0951	12.53±3.0347
O. 1097	.....			2	7	6	8	6	14	14	16	19	9	8	7	3	.....	.....	119	2.385± .0181	12.88± .5725
O. 1098	.....				1	2	1	0	1	0	0	0	1	.....	.....	.....	.....	.....	6	2.117± .0738	12.65±2.5023
O. 1099	.....							1	1	4	2	2	3	0	1	.....	.....	.....	14	2.471± .0326	7.32±1.6792
O. 1100	.....						1	0	0	0	1	0	1	1	.....	.....	.....	.....	4	2.475± .0904	10.82±2.6185
O. 1101	.....			1	0	0	1	2	0	2	0	1	0	0	1	.....	.....	.....	8	2.275± .0741	13.67±2.3478
Total	.....	1	11	37	86	143	167	122	136	187	231	169	131	58	39	12	4	1,534		2.307± .0048	12.48± .1542

[a] Atypical cultures o.1059 and o.1093.

of variation, indicates linkage in the two parents between the factors Yy for stipule width and the Aa factors for flower color. Recombinations in the F_2 of cross-over and noncross-over gametes would account for differences in the range of variation and in the means between the F_2 A and a segregates and the A and a parents.

However, as the combined frequency distributions of the two crosses of Mummy with rogue cultures under discussion (0.1059 and 0.1093) show considerable variation from the F_2 frequency distribution of Gradus as type × Mummy, especially in the position of the respective modes and means, it is unlikely that the factor allelomorphic to x′ in the F_1 hybrid is the x of Gradus type; it is apparently a mutation of X to some other factor for stipule shape, the mutation being analogous to the genetic change occurring when intergrading intermediates are produced from Early Giant types (*1*). In this case the intermediates are of the sort producing few or no rogues among their progeny.

Although the ranges of variation of the two atypical F_2 progenies (0.1059 and 0.1093) overlaps the range of Gradus rogue, no rogues were present in the cultures judging from the character of the F_3 generation. Six F_2 plants of culture 0.1093 from classes 2.05, 2.15, and 2.45 of the variation curve gave only broad and intermediate F_3 segregates. It would appear that the rogue factors which entered the F_1 zygote failed to function as rogue factors at gametogenesis, having mutated to something different from X.

RELATION OF COLOR FACTORS A AND C TO STIPULE SHAPE IN THE TYPICAL F_2 FAMILIES OF THE CROSSES OF MUMMY WITH GRADUS ROGUE

The stipules of 1,404 plants, progeny of the remaining F_2 families (omitting cultures 0.1059 and 0.1093), were measured. The plants represented 49 families, of which the frequency distributions and the derived statistical constants are given in Table XV.

Of the 1,404 individuals, 356 were white (of constitution aa); 305 pink (with A and B factors); and 873 were purple (with A, B, and C factors). The mean stipule ratio of the white segregates was found to be 2.258 ± 0.0110 as compared with 2.336 ± 0.0110 for the pinks and 2.325 ± 0.0063 for the purples (Table VII).

As no essential difference exists between the means of the pink and purple F_2 plants, and as they each contain the A factor, the two color populations may be combined for comparison with the aa segregates. The mean of the AA and Aa plants is 2.335 ± 0.0056 as contrasted with 2.258 ± 0.0110 for the aa segregates, a difference in the means of over 6 times the probable error of the difference.

For a comparison inter se of the frequency distributions of the AA and Aa, and aa segregates and of the F_2 as a whole the number of variates in each class was expressed in percentages of the total number of variates in that particular category of plants. Figure 3 shows the curves obtained by plotting the percentage of variates in each class for the AA and Aa, and aa segregates separately, and for all the F_2 plants irrespective of the color factors present. The graphs for Gradus, Gradus rogue, and Mummy are shown in figure 2, for comparison with the graphs of the F_2 generation.

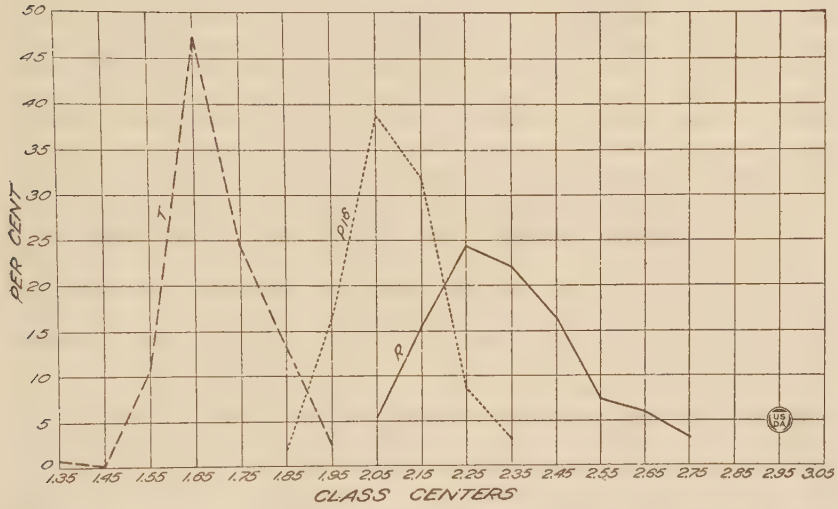

FIG. 2.—Graphs obtained by plotting the frequency distributions, expressed in percentages, of ratio of $\frac{\text{length of stipule}}{\text{width of stipule}}$ for Gradus (T), Mummy (M), and Gradus rogue (R), based on data in Table VIII.

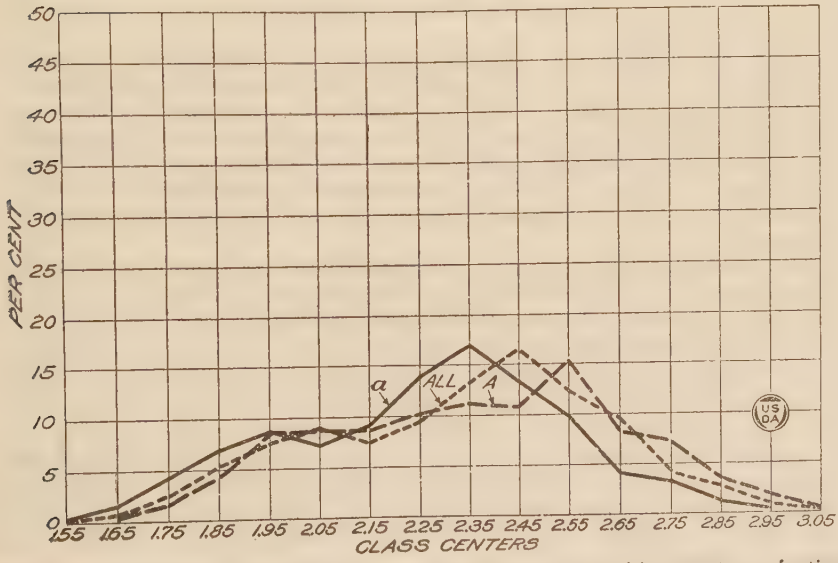

FIG. 3.—Graphs obtained by plotting the frequency distributions, expressed in percentages, of ratio of $\frac{\text{length of stipule}}{\text{width of stipule}}$ for all the F_2 variates of Mummy × Gradus rogue and for the AA and Aa segregates (A) and aa segregates (a) taken separately, based on data in Table VIII.

The majority of variates in a population of Gradus types have a mean stipule ratio between 1.50 and 1.79 and none have been observed with a stipule ratio above 1.99. For Gradus rogue no plants have been found with a stipule ratio of less than 2.00 and by far the greatest number occur between the limits 2.10 and 2.49. The mean stipule range of Mummy extends over portions of the ranges of both Gradus and Gradus rogue, but the majority of individuals occur in classes 1.95 to 2.15, inclusive. Consequently, if linkage existed between the factor for rogue stipules and the a factor for white flowers, one would expect proportionately more of the aa variates to lie close to the mean of the rogue parent, 2.339, and a greater concentration of the variates with the A factor around the mean of Mummy, 2.088, than would be found close to the mean of Gradus rogue. The modes of the frequency distributions of both the colored (AA and Aa) and white (aa) segregates are actually at 2.45, or very near the mean of the rogue parent, however. It is evident, therefore, that no linkage exists between the factor for rogue stipules and the a factor.

The difference in means of the two populations is caused in a large measure by the linkage of the AY and ay factors, so that among the nonrogue segregates the AA and Aa variates tend to have a stipule ratio approaching that of Mummy and the mean of the aa segregates approaches that of the Gradus parent. The effect of linkage is to lower the mean of the aa plants and to increase the mean of the AA and Aa segregates. For this reason more aa segregates than AA and Aa segregates are found in classes 1.55 to 1.95, inclusive. Linkage of the two factors also accounts for the tendency to bimodality that both curves exhibit. (Fig. 3.)

GRADUS ROGUE X MUMMY, AND RECIPROCAL IN THE F_3 GENERATION; CLASSIFICATION OF F_3 FAMILIES

On the hypothesis that Gradus rogues are produced from Gradus by mutation of a single factor, x to X, which is allelomorphic to x′ in Mummy, the expectation in regard to the F_2 rogues of Gradus rogue × Mummy is that approximately 66 per cent will show segregation in the F_3 generation into rogues and nonrogues, while the remaining 33 per cent should breed true. The F_2 broads and intermediates (nonrogues) should not contain rogues among their progeny except as the product of primary mutation.

No record was kept of the F_2 plants saved for seed as to their general appearance, i. e., whether they were rogues, intermediates, or broads. Instead, stipule measurements were made and the stipule ratio was used for a criterion as to which of the three categories, rogue, intermediate, or broad, that the plant belonged. Altogether 184 plants were chosen from a number of F_2 frequency classes (Tables XVI to XVIII). As expected, the parent plants of families containing no rogues came for the most part from classes 1.65 to 2.25. The parent plants of progenies breeding true to the rogue character or segregating into rogues and nonrogues were largely from classes 2.35 to 2.95. This and a classification of seregating F_3 families of Gradus rogue × Mummy and reciprocal are shown in Table XVI.

TABLE XVI.—*Families in which no rogues appeared. Generic constitution of F_2 parents was* x′x′YY, x′x′Yy, *or* x′x′yy

Culture No.	Stipule ratio of F_2 parent.	Broads.	Broads and intermediates.	Intermediates.	Total.
0.279	.....	9	.....	.....	9
0.281	1.65	29	.....	.....	29
0.283	.....	.....	31	.....	31
0.285	.....	.....	.....	13	.....
0.289	.....	.....	16	.....	16
0.291	.....	27	.....	.....	27
0.293	.....	.....	25	.....	25
0.294	.....	.....	16	.....	16
0.296	.....	.....	44	.....	44
0.297	.....	.....	35	.....	35
0.298	1.75	.....	21	.....	21
0.299	.....	18	.....	.....	18
0.300	.....	.....	24	.....	24
0.301	.....	.....	61	.....	61
0.302	.....	.....	49	.....	49
0.303	.....	.....	33	.....	33
0.304	.....	.....	.....	38	38
0.305	.....	.....	.....	37	37
0.306	.....	.....	35	.....	35
0.308	.....	.....	12	.....	12
0.309	.....	.....	37	.....	37
0.310	.....	13	.....	.....	13
0.311	.....	46	.....	.....	46
0.314	.....	21	.....	.....	21
0.315	.....	.....	23	.....	23
0.316	.....	.....	73	.....	73
0.317	1.85	.....	44	.....	44
0.318	.....	.....	21	.....	21
0.319	.....	.....	25	.....	25
0.321	.....	.....	38	.....	38
0.322	.....	.....	91	.....	91
0.323	.....	.....	62	.....	62
0.324	.....	.....	70	.....	70
0.325	.....	.....	20	.....	20
0.326	.....	.....	38	.....	38
0.327	.....	.....	74	.....	74
0.328	.....	.....	11	.....	11
0.330	.....	.....	47	.....	47
0.331	.....	.....	20	.....	20
0.332	.....	.....	22	.....	22
0.340	.....	.....	71	.....	71
0.341	2.05	58	.....	.....	58
0.344	.....	.....	30	.....	30
0.345	.....	.....	47	.....	47
0.347	.....	.....	25	.....	25
0.348	.....	.....	23	.....	23
0.428	.....	.....	75	.....	75
0.429	.....	.....	31	.....	31
0.432	2.25	.....	42	.....	42
0.433	.....	.....	110	.....	110
0.454	2.35	.....	99	.....	99
0.466	2.45	.....	42	.....	42

TABLE XVII.—*Families segregating into rogues and nonrogues. Genetic constitution of F_2 parents was $Xx'YY$, $Xx'Yy$, or $Xx'yy$*

Culture No.	Stipule ratio of F_2 parent.	Rogues.	Nonrogues.	Total.
0.307	1.85	31	11	42
0.329	.....	18	8	26
0.333	.....	?	?	70
0.418	.....	?	?	38
0.420	.....	18	2	20
0.421	2.25	16	3	19
0.422	.....	27	3	30
0.425	.....	31	2	33
0.426	.....	69	4	73
0.431	.....	34	4	38
0.436	.....	18	2	20
0.440	.....	24	3	27
0.441	.....	21	2	23
0.443	.....	19	3	22
0.446	.....	31	6	37
0.450	.....	33	2	35
0.451	2.35	34	3	37
0.453	.....	32	2	34
0.457	.....	57	3	60
0.459	.....	36	2	38
0.460	.....	117	13	130
0.461	.....	64	5	69
0.462	.....	33	4	37
0.465	.....	88	6	94
0.466	.....	25	4	29
0.470	.....	23	5	28
0.471	.....	25	3	28
0.472	.....	14	9	23
0.473	.....	29	3	32
0.474	.....	12	1	13
0.477	.....	13	4	17
0.482	2.45	15	8	23
0.484	.....	29	4	33
0.486	.....	22	6	28
0.489	.....	28	7	35
0.491	.....	24	7	31
0.492	.....	37	9	46
0.493	.....	14	2	16
0.497	.....	19	4	23
0.500	.....	18	2	20
0.502	.....	6	5	11
0.503	.....	16	5	21
0.2419	.....	66	9	75
0.2420	.....	36	5	41
0.2423	.....	28	14	42
0.2424	.....	58	3	61
0.2427	.....	46	3	49
0.2428	.....	25	6	31
0.2429	2.55	26	3	29
0.2430	.....	11	4	15
0.2434	.....	51	2	53
0.2439	.....	?	?	36
0.2441	.....	?	?	11
0.2442	.....	?	?	51
0.2443	.....	6	3	9
0.2444	.....	6	1	7
0.2447	.....	25	2	27
0.2448	.....	18	6	24
0.2449	.....	57	3	60

TABLE XVII.—*Families segregating into rogues and nonrogues. Generic constitution of F_2 parents was Xx′YY, Xx′Yy, Xx′yy*—Continued

Culture No.	Stipule ratio of F_2 parent.	Rogues.	Nonrogues.	Total.
0.2451	.....	49	12	61
0.2452	.....	29	2	31
0.2458	.....	35	2	37
0.2462	2.65	10	2	12
0.2463	.....	15	3	18
0.2464	.....	20	1	21
0.2466	.....	6	2	8
0.2467	.....	9	2	11
0.2468	.....	19	4	23
0.2473	.....	5	4	9
0.2475	.....	34	3	37
0.2476	2.75	31	5	36
0.2477	.....	40	8	48
0.2484	2.85	19	7	26
0.2489	.....	18	1	19
0.2490	2.95	39	5	44
0.2491	.....	25	2	27
Total	.....	2,097	308	.....
0.423 [a]	.....	7	57	64
0.424 [a]	2.25	4	19	23
0.430 [a]	.....	7	23	30
0.439 [a]	2.35	4	33	37
0.455 [a]	.....	3	67	70
0.469 [a]	2.45	4	54	58
0.574 [a]	.....	6	8	14
0.2445 [a]	2.65	13	19	32
0.2470 [a]	.....	12	17	29
0.2482 [a]	2.75	10	14	24
Total	.....	70	311	.....
Grand total	.....	2,167	619	.....

[a] Cultures containing an excess of nonrogues over rogues. The nonrogues were comparable to the intergrading intermediates described by Bateson and Pellew (1).

Of the 184 F_2 plants, 52 had progenies containing (1) only broads, (2) both intermediates and broads, or (3) intermediates only; i. e., they were recessive for the X factor but may have contained the Y or y factor. There were 86 progenies which segregated into rogues and nonrogues; while the progenies of 46 plants were all rogues (Tables XVI to XVIII. The observed number of XX : Xx′ F_2 segregates is very close to that theoretically expected (Table XIX).

Inspection showed segregating families to be of two kinds: First, those with an excess of rogues over nonrogues, and second, those with an excess of nonrogues over rogues. In the latter case the nonrogues were often comparable in appearance to the intergrading intermediates described by Bateson and Pellew (2). Except in cultures containing a very few plants, one would not expect such an excess of recessives as was found in these families.

TABLE XVIII.—*Families in which only rogues appeared. Genetic constitution of F_2 parents was XXYY, XXYy, or XXyy*

Culture No.	Stipule ratio of F_2 parent.	Rogues.	Culture No.	Stipule ratio of F_2 parent.	Rogues.
0.419	.....	55	0.2425	.....	42
0.427	2.25	49	0.2426	2.55	38
0.434	.....	50	0.2435	.....	32
0.442	.....	25	0.2436	.....	61
0.444	2.35	23	0.2437	.....	44
0.445	.....	52	0.2440	.....	41
0.456	.....	30	0.2418	.....	34
0.463	.....	18	0.2446	.....	36
0.476	.....	16	0.2450	.....	16
0.478	.....	29	0.2454	.....	27
0.480	.....	15	0.2455	.....	20
0.481	.....	21	0.2456	.....	33
0.483	.....	18	0.2457	2.65	28
0.485	.....	26	0.2459	.....	31
0.487	2.45	24	0.2460	.....	19
0.488	.....	17	0.2465	.....	51
0.495	.....	20	0.2469	.....	17
0.496	.....	13	0.2471	.....	23
0.498	.....	42	0.2472	.....	18
0.499	.....	39	0.2479	2.75	34
0.502	.....	14	0.2483	.....	44
0.2421	.....	34	0.2486	2.85	15
0.2422	.....	35	0.2487	.....	17

TABLE XIX.—*Ratio of XX : Xx′ plants among 132 F_2 segregates of Gradus rogue × Mummy, as determined from analysis of the F_3 generation, based on data in Table XVII. The expectation is two segregating and one nonsegregating F_3 families*

	Nonsegregating.[a] XX.[b]	Segregating.[a] Xx′[b]	Total.
Observed	46	86	132
Calculated	44	88	132
Difference (D)	2	2	.....
Standard error (S. E.)	3·5	3·5	.....
D/S. E.	·5	·5	.....

[a] Character of F_3 family. [b] Constitution of F_2 parent.

The total number of rogues (2,097) in the cultures containing few nonrogues is obviously far in excess of the total number of nonrogues (308) that would be expected if normal Mendelian segregation occurred in the F_2 plants heterozygous for factors X and x′ (Tables XVI, XVII, XVIII). In the families producing many nonrogues and few rogues the situation is reversed, the cultures containing in all 70 rogues and 311 nonrogues, plainly not in accord with the theoretical, monohybrid 3 : 1 ratio shown in the same tables.

Disregarding the two types of F_3 families and considering all the segregating families as a whole, the observed numbers are: 2,167 rogues (XX and Xx′) and 619 nonrogues (x′x′). The numbers actually found in the two groups show an excess of 78 individuals in the rogue class, a deviation of nearly 4 times the probable error of the difference between the observed and calculated number of variates (Table XX).

TABLE XX.—*Ratio of rogue (XX and Xx′) segregates to nonrogue (x′x′) segregates in all F_3 cultures segregating into rogues and nonrogues, based on data in Table XVII*

	XX and Xx′.	x′x′.	Total.
Observed	2167	619	2786
Calculated	2089.5	696.5	2786
Difference (D)	77.5	77.5	.....
Standard error (S. E.)	22.85	.....	.....
D/S. E	3.4	.....	.....

STATISTICAL STUDY OF STIPULE SHAPE IN THE F_3 FAMILIES OF GRADUS ROGUE X MUMMY, AND RECIPROCAL

Besides classifying the F_3 cultures on the basis of stipule character a number of families were chosen for a statistical study of the stipule shape. A record was kept of whether the families consisted of nonrogues only, rogues, or of both rogues and nonrogues. Table XX shows the frequency distributions and means of the cultures measured. In general the mean stipule ratio of each family tends toward the mean of the category to which the F_2 parent belonged (Table XXI). Thus the means of the x′x′ families tend to approach the mean of x′x′ parent (Mummy) while the Xx′ and XX families have means close to that of the XX parent (Gradus rogue). This tendency in the means of the three types of families is greater if the frequency distributions of the several families belonging to each group be combined. In Table XXII are shown the total frequency distributions from Table XXI of 28 segregating families, of 8 families breeding true to the rogue character, and of 15 families in which no rogues occurred. The mean of the rogue families is 2.503 ± 0.0093 as compared with 2.339 ± 0.0096 for Gradus rogue. The increased narrowness of the stipules of the rogue segregates over that of the rogue parent may be due to the accumulative effect of factors modifying stipule shape such as the Y and n factors responsible for stipule shape and stem fasciation, respectively, in Mummy. The mean of the segregating cultures is 2.259 ± 0.0062 or very near the mean, 2.333 ± 0.0050, of all the F_2 cultures of Gradus rogue × Mummy. For the families in which no rogues appeared the mean is 1.899 ± 0.0053 or intermediate between the means of Gradus type and Mummy, 1.693 ± 0.0107 and 2.088 ± 0.0050, respectively. The mean of the x′x′ families is especially significant as indicating a segregation into Graduslike plants and Mummylike plants among the F_3 plants lacking the X factor. Such a segregation is to be expected in the progeny of F_2 plants of the composition x′x′Yy, and from the effect of lumping together into one frequency distribution the F_3 families with formulae x′x′YY and x′x′yy.

The evidence from the statistical study of stipule shape in the F_3 families points to the homozygous nature of the broad or intermediate F_2 segregates in regard to the x′ factor. In addition the occurrence of F_2 rogues, homozygous and heterozygous for the X factor is also demonstrated by measurement of the stipules of their F_3 progenies.

TABLE XXI.—*Frequency distributions and statistical constants of ratio of* $\frac{\text{length of stipule}}{\text{width of stipule}}$ *for the* F_3 *families of Gradus rogue×Mummy. The rogue families (indicated by R), the nonrogue families (indicated by N), and the families segregating into rogues and nonrogues (indicated by S), are marked in the extreme right-hand column.*

Culture No.	Characters of F_2 parent.	1.45	1.55	16.5	1.75	1.85	1.95	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	3.05	3.15	3.25	3.35	Total.	M.	Coefficient variation.	Classification of F_3 family.
1.279					1	1	4	2	1													9	1.961±0.0245	5.60±0.8931	N
1.281	1.65		2	6	6	10	5															29	1.792± .0136	6.08± .5332	N
1.283				1	11	9	7	3														31	1.850± .0126	5.62± .4829	N
1.285					3	4	6															13	1.873± .0072	2.08± .2649	N
1.289					2	3	4	7														16	1.950± .0178	5.43± .6493	N
1.293	1.75			3	0	3	11	4	4													25	1.950± .0188	7.18± .6884	N
1.294					2	3	2	3	4	1												15	2.056± .0315	9.09±1.0817	N
1.301		1	2	21	16	11	7	1	0	1												60	1.759± .0117	7.65± .5069	N
1.304				2	5	15	4	3	1	2	0	1	2									35	1.941± .0247	11.17± .9036	N
1.306				1	1	2	6	13	7	2												32	2.050± .0137	5.65± .4778	N
1.307					5	6	4	7	5	3	7	2	3									42	2.231± .0247	10.67± .7941	N
1.309	1.85	1	1	0	0	0	11	12	7	2	1	2										37	2.050± .0184	8.09± .6393	S
1.314				1	7	7	6															21	1.864± .0035	1.28±1.3325	N
1.329					2	4	4	6	3	2	3	0	1	0	1							26	2.089± .0349	12.63±1.2000	S
1.308					2	3	2	0	3	2												12	1.991± .0348	8.99±1.2491	N
1.325				2	6	6	10	7	4													35	1.925± .0133	6.07± .4854	N
1.341				2	6	16	11	7	1													43	1.917± .0114	5.79± .4225	N
1.342	1.95				2	2	3	2	2	7	10	10	0	3	1	2						44	2.308± .0262	11.17± .8131	S
1.343								1	2	4	3	4	2									16	2.331± .0239	6.09± .7179	R
1.346				2	2	10	14	8	1	3	2	1	0	2	1							46	2.124± .0239	11.34± .8076	S
1.347					1	7	7	5	2	2	1											25	1.990± .0199	7.43± .7127	N
1.333	2.15				3	0	0	5	11	12	16	10	5	5	1	2						70	2.336± .0179	9.54± .5487	S
1.418					3	3	8	4	4	6	5	3	1									37	2.117± .0242	10.01± .7919	S
1.419								1	7	7	10	14	10	4	1	1						35	2.427± .0140	6.34± .4093	R
1.423	2.25				3	4	9	9	11	10	7	3	5	1	2							64	2.071± .0196	11.26± .6786	S
1.425					1	1	1	4	5	4	3	7	3	2	1	1						33	2.207± .0328	12.68± .0695	S
1.428						2	9	12	1	1												25	2.010± .0066	2.43± .2319	N
1.430					3	5	8	4	1	0	1	0	2	1								25	2.022± .0308	11.32±1.0930	S
1.445				1	6	6	9	9	1	3	1	4	2	0	2	0	0	1				45	2.132± .0297	13.88±1.0057	S
1.446	2.35			1	2	7	2	3	5	9	3	3	1	0	1							37	2.068± .0248	10.69± .8477	S
1.450					3	3	5	9	4	3	2	3	2	1								35	2.138± .0261	10.71± .8741	S
1.458						6	7	8	12	7	6	1	0	2								49	2.128± .0168	8.22± .5638	S
1.467	2.45			1	1	2	8	2	7	4	7	3	3									38	2.165± .0267	10.77± .8429	S
1.2437									1	5	9	2	6	10	3	5	2	1				44	2.606± .0220	8.32± .6023	R
1.2438								2	0	1	3	3	2	3	1	1						16	2.362± .0364	9.99±1.2041	S
1.2440	2.55							1	0	1	5	6	7	18	3	0	0	1				42	2.462± .0147	5.76± .4253	R
1.2441					1	1	3	1	1	3	0	3	1									14	2.164± .0440	11.27±1.4548	S
1.2442				2	3	9	3	5	7	8	10	2	1									50	2.126± .0294	14.58±1.0041	S

I.2449	2.65	....	....	....	1	0	2	4	4	2	7	8	9	9	3	1	....	....	....	....	....	50	2.418± .0231	10.04± .6812	S
I.2451		....	....	2	2	3	6	7	5	12	7	6	4	2	1	0	1	....	....	....	....	58	2.229± .0231	11.71± .7433	S
I.2452		....	....	....	....	1	1	2	1	3	4	4	4	2	2	1	....	....	....	....	....	25	2.394± .0337	10.41±1.0067	S
I.2454		....	....	....	....	....	....	....	4	2	3	7	6	1	2	0	2	....	....	....	....	27	2.469± .0259	8.10± .7483	R
I.2455		....	....	....	....	....	....	2	1	2	4	2	5	1	2	1	....	....	....	....	....	20	2.440± .0322	8.77± .9442	R
I.2456		....	....	....	....	....	....	....	....	2	2	5	9	5	4	3	2	0	2	....	....	34	2.562± .0270	9.13± .0191	S
I.2458		....	....	....	....	....	1	2	4	0	2	3	6	6	3	5	0	1	....	....	....	33	2.462± .0321	11.29± .9495	S
I.2470		....	....	....	2	0	2	1	0	3	1	5	3	4	0	1	....	....	....	....	....	22	2.359± .0451	13.31±1.3772	S
I.2472		....	....	....	....	....	....	....	1	0	3	0	1	3	4	2	5	2	....	....	....	21	2.727± .0348	9.05± .9442	R
I.2476		....	....	....	....	....	1	0	4	4	10	8	4	2	1	1	....	....	....	....	....	35	2.392± .0203	7.44± .6031	S
I.2477	2.75	....	....	....	....	....	....	....	3	3	1	4	6	6	6	6	2	4	3	0	2	46	2.709± .0303	11.25± .8010	S
I.2483	2.85	....	....	....	....	....	1	2	0	2	3	4	5	6	10	4	5	1	0	1	1	45	2.652± .0282	10.59± .7614	S
I.2490	2.95	....	....	....	1	0	0	5	2	3	2	2	2	6	5	4	4	1	0	0	1	38	2.556± .0392	13.26±1.0438	S

TABLE XXII.—*The combined frequency distributions and derived statistical constants of ratio of* $\left\{\frac{\text{length of stipule}}{\text{width of stipule}}\right\}$ *for the rogue (R), segregating (S), and the nonrogue (N) families of the F_3 generation from cross Gradus rogue × Mummy based on data in Table XXI.*

Cultures, No.	Classification.	1.45	1.55	1.65	1.75	1.85	1.95	2.05	2.15	2.25	2.35	2.45	2.55	2.65	2.75	2.85	2.95	3.05	3.15	3.25	3.35	Total.	M.	s.	Coefficient variation.
8	R	....	....	....	....	....	1	4	17	27	40	41	57	27	16	12	12	3	1	....	....	258	2.503±.0093	0.2230±.0066	8.89±.2655
28	S	1	1	13	47	84	120	130	119	119	121	108	73	61	41	29	12	8	3	1	4	1,095	2.259±.0062	.306±.0044	13.54±.1911
15	N	1	4	37	64	87	97	64	27	9	1	....	....	....	....	....	....	....	....	....	....	391	1.899±.0053	.154±.0037	8.81±.2141
Total		2	5	50	111	171	218	198	163	155	162	149	130	88	57	41	24	11	5	1	4	1,745			

DISCUSSION OF RESULTS.

True-breeding hybrids have been found in other genera than Pisum, notably in *Oenothera*, and have been interpreted by Muller (*10*) as due to the action of balanced lethal factors. In self-fertilized Gradus plants there is no evidence of zygotic lethals since under proper growing conditions all the ovules in a pod develop. Although an occasional sterile rogue is met with, all ovules generally form viable seed. In over 60 instances crosses between Gradus and Gradus rogue gave an average of 4.5 seeds per pod out of a possible 7 or 9. About 4 seeds per pollination is the number generally obtained from artificial crosses of Gradus with other varieties. However, it has been customary to pollinate two or three stigmas with the pollen of one flower, the result being one well filled pod and one or two partially filled, as a consequence of deficient pollination.

A microscopical examination of the pollen of Gradus and Gradus rogue showed well-developed pollen grains in both forms. Their pollen is about 100 per cent perfect. There was no morphological evidence of defective pollen which might be interpreted as due to the action of gametic lethals.

It is, therefore, apparently out of the question to explain the anomalous behavior of the rogues in crosses with Gradus types as due to the presence of zygotic or gametic lethals.

As previously stated, the nonappearance of Gradus segregates in the F_2 generation of the cross Gradus with Gradus rogue is explained by Bateson and Pellew (*1*) as probably due to somatic segregation of the type and rogue "elements" in the F_1 hybrid. The same authors have not suggested, however, a mechanism by which somatic segregation is accomplished. Such segregation would occur if somatic nondisjunction took place early in the development of the F_1 plants, so that of the two daughter cells formed, one would receive both of the chromosomes derived from one member of the heterozygous chromosome pair present in the parent cell, and the other daughter cell would receive the two chromosomes derived from the second member of the heterozygous pair. As a result, both cells would retain the characteristic number of somatic chromosomes and at the same time be homozygous for either the type or rogue factors.

Besides assuming the phenomenon of somatic nondisjunction, the further assumption must be made that the daughter cells homozygous for the rogue factors increase more rapidly than cells containing the type factors, and consequently the F_1 plant becomes more roguelike as it matures. At sporogenesis only rogue tissue would take part in gamete formation; therefore type plants would not appear among the F_2 progeny.

Although somatic nondisjunction offers a hypothesis to account for somatic segregation it does not explain satisfactorily the failure of the type factors or "elements" to be present in the gametes of the F_1 hybrids. Certainly accepted instances of somatic nondisjunction are rare, the best examples being the gynandromorphs in *Drosophila* described by Morgan and Bridges (*9*) and attributed to the effect of the dropping out of the sex chromosome at an early division of the fertilized egg. The demonstration of the loss of a chromosome was possible from a knowledge of the factors linked with sex. As there are no factors known which are linked to the type allelomorphs of the rogue factors, the loss, by nondisjunction in the F_1 hybrid, of the chromosome carrying the type factor can not be detected. In addition, in the F_1 plants nondisjunctional

nuclear divisions would have to take place too regularly and too often to make the explanation seem reasonable.

As an alternative hypothesis, the idea of "mass" somatic mutation is advanced to account for the anomalous behavior of the rogues in heredity. Using the factor symbols here adopted the x factor of Gradus is assumed to mutate occasionally to the X factor of Gradus rogue. The factor pair xx when in a homozygous condition is relatively stable and mutation to X rarely takes place. However, the heterozygous Xx combination is very unstable and x mutates with great frequency to X, creating a homozygous and more stable condition of the germplasm in regard to the X factor. Mass somatic mutation of x to X occurs in the soma of the F_1 hybrid at an early stage in its development and would account for the prevailing absence of the x factor among the F_1 gametes. The same phenomenon would be true of Gradus plants in which the primary mutation of x to X took place. Such a mutation occurring early in the ontogeny of a Gradus type plant would produce an individual which would gradually become more roguelike as it matured. Or when the mutation takes place late in the development of the plant, the form of the individual would not necessarily be changed but the issue derived from the cell containing the X factor, would, if it entered into gamete formation, cause rogues to appear in the next generation.

The fact that occasionally an F_1 hybrid of Gradus × Gradus rogue is Graduslike at maturity rather than roguelike is interpreted as indicating that rare Gradus gametes are produced, as a consequence of mutation or otherwise, in which the X factor is replaced by an allelomorph comparable in stability to the x′ of Mummy.

It is probable that the rogues are an extreme manifestation of a series of mutations originating by changes in the x factor of Gradus. Thus the various sorts of intergrading intermediates described by Bateson and Pellew (1) may well represent various modifications of the factor x which may be designated as x″, x‴, etc. The xx″ or x″ x″ combinations produce intergrading intermediates in which mutation of either of x or x″ to X is more frequent than in Gradus type. The differences in the stability of the various modified x factors as exhibited in the rate of change of these factors to X, accounts for the existence of high and low rogue-producing strains of intermediates.

The difference in the proportion of rogues produced from the lower as compared with the upper nodes of intergrading intermediates, besides being due to a multiplication of the somatic cells in which a primary mutation of x to X has occurred, may conceivably be caused by an increase in the number of somatic mutations brought about by physiological changes in the protoplasm as the plant matures.

The mutation of x to X in Gradus, in the F_1 hybrid and in the intergrading intermediate is comparable to what Emerson (5) calls a recurring somatic mutation. The varieties in which rogues arise are of the sort earlier described by de Vries (13) as "ever-sporting," meaning that it is impossible to free the stock of the tendency to produce "sports" (mutations).

The results in the F_2 generation of crossing Gradus type with Mummy and Gradus rogue with Mummy have led to the assumption of a factor pair Yy in addition to the xx factors as partly responsible for stipule shape in Gradus and Gradus rogue. In Gradus there are at least two factor pairs xx and yy determining the ratio of width to length of stipule.

The y factor in Gradus is linked with the a factor for white flowers; its allelomorph Y is linked with the A factor for colored flowers in Mummy. The proof of the presence of two factors for stipule shape in Gradus and Gradus rogue lies in the fact that no linkage exists between the X factor (the mutated form of the x factor of Gradus) in Gradus rogue and the a factor for white flowers as determined from an analysis of the F_2 generation of the cross Gradus rogue with Mummy.

The allelomorph, in Mummy, of factor x is probably not identical with x but is very similar in its somatic expression. At least in combination with y of Gradus (the x′x′yy segregates from the F_2 generation of Rogue × Mummy), the x′x′yy plants have stipules very nearly like Gradus type. The factor allelomorphic to x and found in Mummy is called x′ to distinguish it from the x factor of Gradus. Additional evidence of a difference between x and x′ is the fact that x′ has never been known to mutate to X when x′ is present in the homozygous state. The factor x′ is apparently more stable than x.

In addition to the assumed inherent stability of the x′ factor found in Mummy it is probable that the Y factor also acts as a stabilizer of the germ plasm. The heterozygous F_1 plants of Gradus rogue × Mummy (YyXx′) have a germ plasm which is certainly less affected by the presence of the X factor than is the heterozygous Xxyy germ-plasm of Gradus rogue. With the Xx′ combination, recurring somatic mass mutation to the extent obtaining in the F_1 generation of Gradus type × Gradus rogue, does not occur. The various factors that entered the zygote take part in gamete formation at maturity and give rise to the expected F_2 combinations. Although Y behaves as a stabilizer of the F_1 germ plasm and retards mass mutation of x′ to X, the extent of the influence is difficult to determine. Nor is it known to what extent, if any, senility affects the relation of the X and x′ factors. It is possible that, with increasing age, the F_1 plants exhibit a change in the mutability of x′ to X, resulting in an increase of rogues among the F_2 segregates. Since other disturbing causes than somatic mutation in the F_1 hybrid may combine to upset the expected number or ratio of F_2 recombinations, the deviations of the observed number from the calculated number of variates in any one class can not be used, for the F_2 data at hand, to approximate the rate of change of x′ to X.

That changes in the X factor may occur in the F_1 hybrids here discussed is indicated by the exceptional F_1 plant (no. 9.727-6), which was similar in appearance and genetic behavior to the F_1 hybrids of Gradus type × Mummy. Additional evidence of mutation of X to some other form is shown in the behavior of two roguelike F_1 plants (No. 9.722–1 and No. 9.722–5). These plants apparently produced very few, or no, rogues in the next generation (families 0.1059 and 0.1093). The primary mutation or mutations of X in the F_1 parents was here delayed until late in development and, while not affecting the soma, radically changed the genetic character of the microspores and macrospores.

An analysis of the F_3 generation of the cross Gradus rogue with Mummy substantiates the hypothesis of Mendelian inheritance of the rogue factors complicated by recurring somatic mutation. The number of segregating to nonsegregating F_3 families is in close agreement with the theoretical number of 1 XX : 2 Xx′ F_2 rogue segregates expected from a monohybrid F_1 generation. The ratio of XX to Xx′ plants in the progenies of heterozygous F_2 rogues is disturbed by the phenomenon of recurring somatic mutation.

The discrepancy between observation and theory is great in respect to the ratio of rogues to nonrogues in the segregating F_3 families. However, the fact of segregation is considered more important than the ratios obtained. The instability of the heterozygous Xx′ combination, though not leading to a complete elimination of the x′ gametes, by mutation of x′ to X, is such as to produce an excess of X gametes over the number that would normally be formed if somatic mutation did not take place.

SUMMARY

(1) The Gradus variety of *Pisum sativum*, characterized by broad, wavy, emarginate stipules with a mean ratio of $\frac{\text{length of stipule}}{\text{width of stipule}}$ of 1.70, occasionally produces rogue mutations, characterized by narrow, flat, pointed stipules with a mean ratio of 2.35.

(2) Primary rogues are produced from Gradus types by a mutation of a single factor x to X. They are therefore heterozygous, of the formula xX. They give an F_2 of homozygous secondary rogues, XX, through recurrent (mass) somatic mutation of the x factor to X. Such recurrent mutation is believed to occur because of the instability of the combination of xX.

(3) The crosses Gradus × Gradus rogue, and reciprocal, likewise produce an unstable F_1 germ plasm in which mass, somatic mutation of x to X occurs.

(4) The effect of mass somatic mutation in the F_1 hybrid is to produce a germ plasm homozygous for the X factor in by far the greater number of the somatic cells. At gametogenesis only an occasional x gamete is produced. The F_2 generation consists almost entirely of rogues (XX), the Gradus type (xx) very rarely appearing.

(5) In addition to the x factor a second factor y for stipule shape is present in both Gradus and Gradus rogue. The factor y is linked with the a factor for white flowers.

(6) The English Mummy pea, a nonrogue producing variety, has a stipule ratio of 2.05 determined by a factor Y, allelomorphic to y of Gradus, and linked with the A factor for colored flowers.

(7) In crosses between Gradus and Mummy the number of cross-overs between AY and ay is approximately 20 per cent.

(8) Mummy, in addition to the Y factor, has a factor x′ which is allelomorphic to the x factor in Gradus type, therefore to the X factor of Gradus rogue. The x′ factor is practically identical with the x factor in its expression but differs in that it only rarely mutates to X, even in the combination x′X.

(9) The germ plasm of the F′ cross, Gradus rogue (yyXX) × Mummy (YYX′x′) is fairly stable. In the F′ hybrids, YyXx′, the factor x′ mutates to X but not to such an extent as to prevent at gametogenesis the formation of the usual gametes, XY, Xy, x′X, and x′y, as indicated by the appearance in the F_2 generation of rogues (having the X factor), Graduslike plants (having the x′ and y factors), and Mummylike segregates (having the x′ and Y factors).

(10) The expected 3 : 1 ratio of rogues to nonrogues in the F_2 and succeeding generations obtained from the heterozygous Xx′ plants, is disturbed by an excess of X gametes and consequently of XX and Xx′ zygotes.

(11) Inheritance of the factors for stipule shape X and y in Gradus rogue is Mendelian. Normal inheritance is obscured by somatic mutation of the factors x and x′ when in the Xx or Xz′ combination.

(12) In addition to determining a stipule ratio of 2.05 in Mummy, the factor Y acts as a stabilizer of the germ plasm. Somatic mutation of x′ to X in the F_1 cross between Mummy and Gradus rogue (Xx′Yy) does not take place to the extent in which mutation of x to X occurs in the F^1 crosses between Gradus type and rogue (XxYy) on account of the presence of the Y factor.

(13) Besides mutations of x and x′ to X, other mutations of x and x′ occur which affect stipule shape. The nature of the latter kind of mutations has not yet been investigated.

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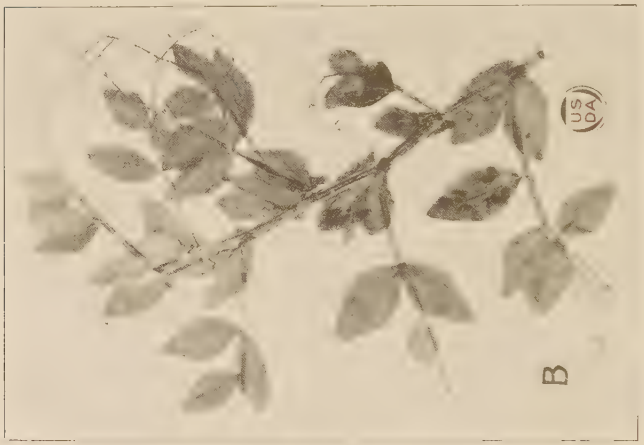
PLATE 1

A.—Upper part of a mature type plant of Gradus. × ¼.
B.—Upper part of a mature rogue plant of Gradus. × ¼.

B

A

C


B

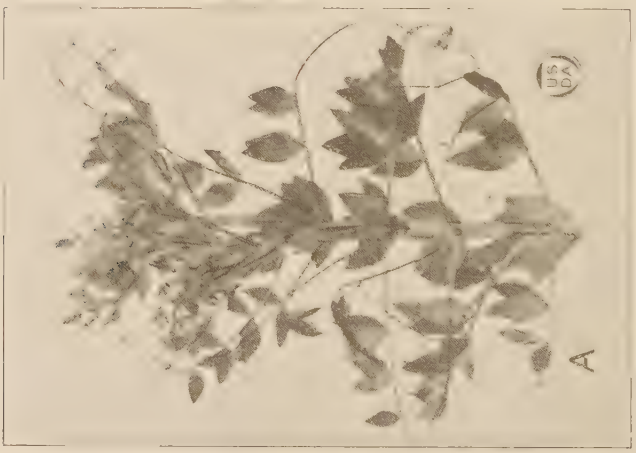

A

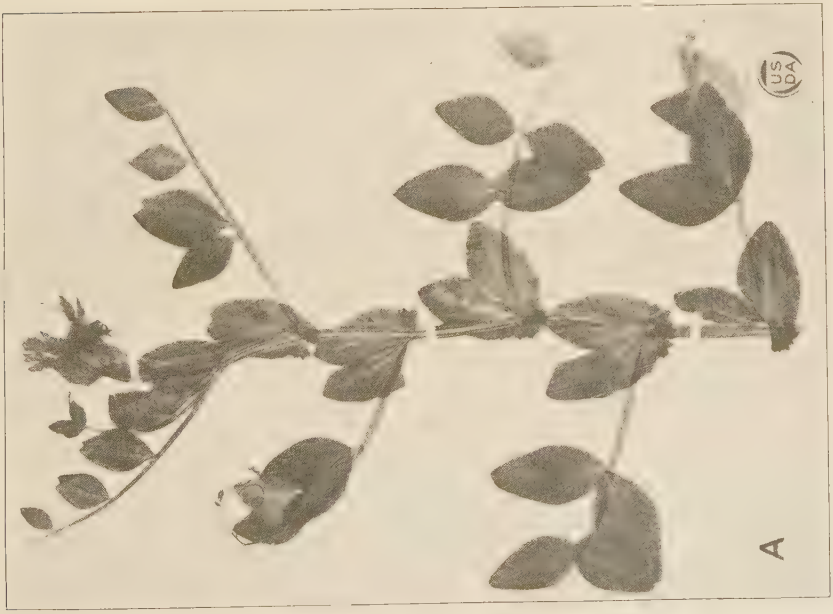
PLATE 2

A mature plant of the Mummy variety (P16).
A.—The tip. $\times 1/5$.
B.—The part immediately below the portion shown in A. $\times 1/5$.
C.—Lower part of the stem. $\times 1/5$.

PLATE 3

A.—Upper part of a branch of a mature F_1 plant of Gradus type × Mummy. × ¼.
B.—Upper part of a branch of a mature F_1 plant of Gradus rogue × Mummy. × ¼.

B


A

B

A

PLATE 4

A.—Upper part of a mature broad (y) segregate from the F_2 generation of Gradus type × Mummy. Note the typelike emarginate stipules. × ¼.
B.—The part immediately below the portion shown in A. × ¼.

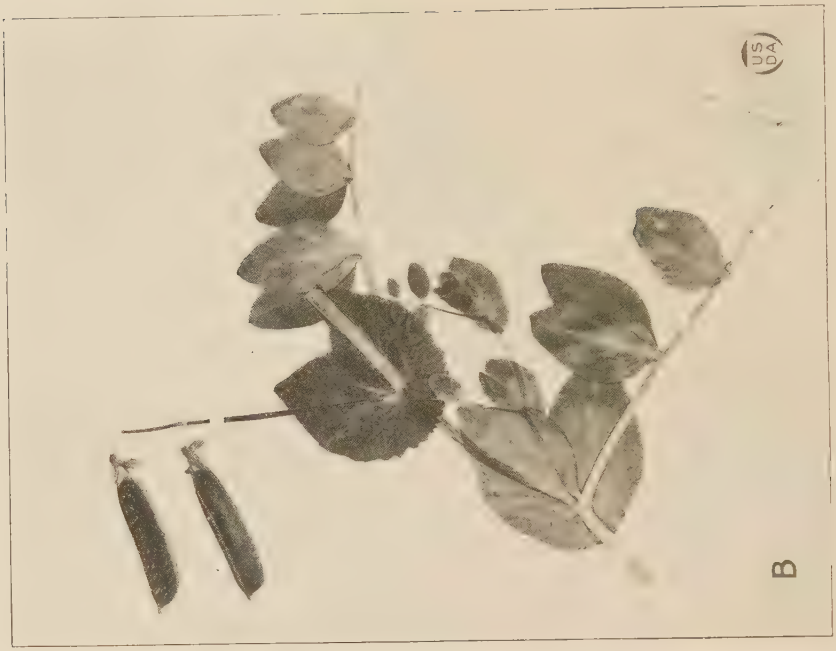
PLATE 5 [a]

A.—Upper part of an intermediate (Y) or Mummylike segregate from the F_2 generation of Gradus type × Mummy. Note the narrow pointed stipules. × ¼.
B.—The part immediately below the portion shown in A. × ¼.

[a] Plates 4 and 5 are of plants from the same F_1 family.

B

A


(USDA)
B

(USDA)
A

PLATE 6

A.—Upper part of a mature broad segregate from the F_2 generation of Gradus rogue × Mummy. × ¼.
B.—The part immediately below the portion shown in A. × ¼.

PLATE 7

A.—Upper part of a mature intermediate segregate from the F_2 generation of Gradus rogue × Mummy. × ¼.
B.—The part immediately below the portion shown in A. × ¼.

USDA
B

USDA
A

B

A

PLATE 8 [b]

A.—Upper part of a mature rogue segregate from the F_2 generation of Gradus rogue × Mummy. × ¼.
B.—The part immediately below the portion shown in A. × ⅓.

[b] Plates 6, 7, and 8 are of plants from the same F_2 family.